

Bridging Biological Systems with Social Behavior, Conservation, Decision Making, and Well-being through Hybrid Mathematical Modeling

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To Betty Sullens for guiding me in resilience, independence, and perseverance .

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*“Success is to be measured not so much by the position that one has reached in life
as by the obstacles which he has overcome.”*

– Booker T. Washington

Abstract

Mathematical modeling can achieve otherwise inaccessible insights into biological questions. We use ODE (ordinary differential equations) and Game Theory models to demonstrate the breadth and power of these models by studying three very different biological questions, involving socio-behavioral and socio-economic systems, conservation biology, policy and decision making, and organismal homeostasis.

We adapt techniques from Susceptible-Infected-Recovered (SIR) epidemiological models to examine the mental well-being of a community facing the collapse of the industry on which it is economically dependent. We consider the case study of a fishing community facing the extinction of its primary harvest species. Using an ODE framework with a complex contagion process, we track the mental health states of people as they shift to a sustainable source of income. We find that community connectivity has a meaningful impact on both the duration and transition dynamics.

Successful preservation of threatened species can depend on the appropriate deployment of limited resources to combat illegal poaching. Using mathematical game theory based on the ‘Colonel Blotto Game’, we model the battle between Conservationists and Poachers. Conservationists must allocate social, political, and financial resources to curtail poaching while Poachers can expend resources to nullify Conservationist activities in each of these ‘battlefields’. We analyze payoffs and player budget distributions to determine overall player success to provide novel tools for policy/decision support and improve efficacy in planning conservation strategy.

Recent advances in the field of stress physiology have presented the reactive scope model: a conceptual theory that extends beyond traditional homeostatic models to incorporate influences physiological state and life history on an animal's ability to respond to stressors. A recently published quantitative model of the reactive scope model made simplifying assumptions about types of energetic resources and how they are used and replenished [Wright et al., 2023]. We extend that model meaningfully by considering a realistic energy budget and the consideration of multiple mediators simultaneously. This improves the capabilities of the model to predict an animal's health outcomes from exposures to stressors over time.

Together, these models demonstrate the power of modeling to advance understanding in fields ranging from population health to conservation to physiology.

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Chapter 1

How an Industry Collapse Affects Community Mental Health: a Complex Contagion Model

1.1 Abstract

We adapt techniques from epidemiological models to examine the mental well-being of a community facing the collapse of the industry on which it is economically dependent. We consider the explicit case study of a fishing community facing the population collapse of its primary harvest species. By using an ordinary differential equation (ODE) susceptible, infected, recovered (SIR) framework with complex contagion processes, we track the movement of people through different mental health states as they shift their efforts to a more sustainable source of income by either changing harvest species or switching careers entirely. State changes occur due to either the direct observation of the declining harvest population or by interaction with other community members. We present three different possible scenarios for the decline of the harvest species, along with two effort functions to capture how fishermen may approach harvesting. We also present sensitivity of system behavior to different underlying mechanisms causing harvest species decline, potential conservation efforts, and the social connectivity of the community. We find that community connectivity has a meaningful impact on both the duration and transition dynamics, suggesting that interventions to support such communities may be most effective by focusing on socio-behavioral interventions.

1.2 Introduction

There are unique psychological and social stresses associated with changes in the viability of an industry that supports a community. Previous studies have looked at small business ownership, threats to the survival of small businesses, and the mental health of the people involved in the face of crisis [115, 108]. Recent models have looked at different types of stressors. One paper focuses on business owners during a crisis (such as the COVID-19 pandemic) and developed a model presenting five stages of grief [108]. This work demonstrated that although people may experience

intense psychological stress moving through the stages of denial, anger, bargaining, depression, and acceptance, people also display resilience and adaptability in the face of change. [81] instead looked at the resilience of a community in the face of a natural disaster. Previous studies have also used mathematical epidemiology models to analyze the mental well-being of communities experiencing the spread of physiological stress and the impact that it has on people’s happiness. For example, [57] used a SIR (susceptible, infected, recovered) framework to track how psychological stress moves through a population in the face of the COVID-19 disaster. The authors split the stressed class into two states: those who are physically/mentally stressed and those who are instead financially stressed. A basic reproduction number, disease-free equilibrium, and endemic equilibrium were calculated and, through numerical results, it was shown how alteration in parameters could affect recovery. They concluded that different methods such as yoga, exercise, and meditation could offer effective interventions to support people’s mental well-being. Another study by [120] looks at how factors such as exercise, mental resilience, and positive emotions are intertwined.

Here, we explore the linkages between the long-run viability of a renewable resource based industry and the mental well-being of communities supported by the resource. We consider a community supported by a biological resource that is itself facing inevitable extinction. Following [57], the psychological stress facing the community is modeled as layered simple and complex contagion processes that consider multiple exposures. Understanding the linkages is important for the advanced targeting of public health programs in communities facing resource extinction or transition.

Bio-economic models integrate biological and economic processes to understand the economic incentives associated with renewable resource exploitation and the key role of economic institutions in explaining or predicting economic events [24]. They have been used to examine how a market would be affected by scenarios such as a crisis, and how policies such as regulation could be used to adjust economic behavior

in the face of risk [92, 6]. In addition, bio-economic models have looked at how species extinction and economic incentives are connected [40, 29, 113].

Within the bio-economic literature, there is a long history of attempting to explain the economic incentives (and disincentives) surrounding extinction in fisheries [22, 23, 25, 15]. There are also numerous examples of how to manage economic incentives and conserve species such as [90] and [59], based on the application of tools in dynamic optimization.

Here, we consider a more ecologically relevant scenario through a compromise between ecological and economic priorities and the introduction of a SMS (safe minimum standard). We examine how different approaches to the same issues can be at odds with each other, preventing true optimization in either biology or economics. However, across studies, even when the stress decreasing natural resource levels can put on a community's economic health is considered explicitly, resource preservation and/or sustainable use is usually the goal. To the best of our knowledge, the mental well-being of a community facing the unavoidable demise of its primary harvest species has yet to be studied.

In this paper we consider the mental health of a fishing community that is reliant on a doomed harvest, meaning the harvest is not recoverable, so long-run conservation is a fruitless endeavour. People are social creatures whose thoughts and actions are affected by the interactions they have with others. Other studies have looked at the spread of ideas similar to how a disease is spread, but including interactions with multiple people and how these interactions affect idea adoption differently compared to previous work is a valuable addition [3]. The occurrence of community stress has been studied in areas such as urbanicity, where biometric data and diary entries are used to label stress [94]. Also, [4] looks at how life-altering stressors, such as cancer, impacts a person's well-being and ability to adjust. Both studies explicitly consider how stress puts strain on both individuals and the community as a whole. Communities can experience stress differently depending on how connected the members of the community are to each other and how strong the sense of community

is among them. Social connectivity of a community is a strong indicator of the mental health of the community [100]. Additionally, strongly connected communities have better success overcoming disasters [81]. We study how social interactions affect the way people move through different mental states (non-stressed, stressed, and recovered), explicitly examining the average time a person spends stressed, the peak number of people stressed at the same time within the community, the duration of the community transition through the crisis, and how many people were able to avoid ever passing through the stressed state due to reliance on supportive community dynamics.

The objective of this paper is to provide insight into how a community could be affected by the unavoidable exhaustion of a diminishing natural resource (here specifically, the extinction of a harvested species). We examine how different factors such as community connectivity, different harvest methods, and different processes driving the underlying species decline affect the dynamics of the community's transition to an alternative income source, along with the mental health of the population during the transition. This research can provide valuable insight for policymakers and government agencies looking at how to allocate financial aid to people in need, and which potential actions might best support a community during such a transition.

1.3 Methods

Species conservation has been well studied, including many models analyzing population dynamics and parameters affecting those dynamics [7, 89]. The spread of contagions can be described as either simple or complex [80]. A simple contagion only requires one interaction to induce a state change or adopt the contagion, while a complex contagion requires multiple exposures to induce the same transition. Simple contagions are common in epidemiological studies and often use the mathematical techniques of SIR, SIS, and/or SIRS models [12]. The spread of ideas is more

frequently studied using complex contagion processes. For example, [104] uses a complex contagion model to study social media interaction on Twitter via retweets. The model presented here follows the idea of [80] in combining a simple contagion and a complex contagion to better represent both specific biological and social dynamics.

The complex contagion model considered here analyzes how stress affects the mental health of a community dependent on a doomed harvest. We consider the specific case study of a fishing community dedicated to the exploitation of a species that is on an inevitable trajectory of depletion (or extinction) such that continued exploitation will provide insufficient income for the fishermen in the community. Although this model is built around a community supported by a fishery, it can easily be adapted to other natural resources (as further described in the Discussion below).

There are a few assumptions critical to the development of the model. The community exploits the species as a common property resource with a well-defined sharing rule where each fisherman gets an equal share of the catch. In addition, the species is on a trajectory of inevitable extinction and it is unrecoverable, meaning that conservation efforts can delay but not avoid extinction. Due to this, the fishermen must eventually make a transition to an alternative source of income, whether that be in the form of shifting to fishing a different species or a complete career change. Fishermen can enact this shift either by passing through an unhealthy stressed state themselves, or by interacting with community members and gleaning from the stress experiences of others the insight that they should anticipate and avoid personal stress by proactively transitioning income sources. The time unit is chosen to be in years to approximate transitory dynamics in studies of fish population decline and economic system dependency transitions in industry [55, 17]. Our model provides an opportunity to explore how the connectivity of a community affects the mental health of the community and if conservation or aid should be provided to slow the decline of the fish population to reduce mental strain on the community.

1.3.1 Species Population Decline

The fish population is taken to be in a state of decline that will eventually reach critically low numbers or extinction. We provide three different scenarios in which this can occur.

First, we consider a scenario in which the lower the fish population gets, the faster it declines. The population ODE is represented by the following:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - qEx \quad (1.1)$$

where $x(t)$ represents the fish population at time t , K is the carrying capacity of the habitat, q is the catchability of the species, E is the fishing effort, and r is the population growth rate which is defined to be negative in this scenario. This is the only scenario with the requirement that r is negative, which presents a unique circumstance. The scenario reflects a situation that could occur to a species affected by a disease impacting reproduction, such as Brucellosis among cattle, which has been devastating to farmers due to the disease's high rates of morbidity and resulting lifetime sterility [62]. This widespread disease causes revenue loss along with psychological stress for people dependent on the herd. Additionally, in stone loach, there is evidence of a positive correlation between parasite susceptibility and reproduction investment, which then leads to a trade-off between reproduction and immune investment [107].

The second scenario we address is one in which the environmental carrying capacity is reduced due to a factor such as habitat loss (i.e., reducing the size of the population the environment can support). The following ODE captures this scenario.

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K(t)}\right) - qEx \quad (1.2)$$

Note that $K(t)$ is a function rather than a value. Different functions can be used to represent different systems, here we employ $K(t) = K_0(1 - b)^t$ where K_0 is the

initial carrying capacity and $b \geq 0$ is the rate of habitat loss. Unlike Equation 1.1, in equation 1.2, a growth rate is adopted which allows $r > 0$.

Lastly, we consider a scenario in which the species faces an exogenous increase in the rate of mortality which could be caused, for example, by pollution. Equation 1.3 captures this scenario where m is the portion of fish removed.

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - mx - qEx \quad (1.3)$$

In this scenario, $r > 0$ while $r \left(1 - \frac{x}{K}\right) < m + qE$, such that more fish are being removed than added to the population.

In equations 1.1, 1.2, 1.3, fishing effort (E) is the effort expended by fishermen to catch fish and can be explicitly defined in many ways. Here we focus on how effort depends on community characteristics, in terms of the population of non-stressed fishermen, $N(t)$, the population of stressed fishermen, $S(t)$, and the population of fishermen that have transitioned to a different form of income, $R(t)$, referred to as recovered individual moving forward.

We consider a situation in which the exploitation of the species by fishing has a relatively small effect on mortality in comparison to the pressures leading to the inevitable decline. In addition, the institutional failures seen in fisheries as a class of common property problems are assumed to not exist or have been resolved [77]. In this setting, we do not focus on the incentives facing fishermen to exploit the fishery, but rather on the effect of different types of fishermen who exploit the fishery. Two scenarios are considered. In the first, fishing effort is 1.4 which is simply the total number of people fishing the species, represented by the non-stressed and stressed fishermen population.

$$E = N + S \quad (1.4)$$

Harvests are restricted by the existing population, $q(N+S) \leq 1 \implies q \leq \frac{1}{N+S}$. In the second scenario, stressed fisherman are so concerned by the threat to their livelihood that they (ultimately futility) increase their effort as they realize the severity of the

situation.

$$E = N + \frac{\rho(S)}{1 + e^{(\lambda x - \mu)}} \quad (1.5)$$

Equation 1.5 allows stressed fishermen to do the work of a maximum of ρ people. λ is the rate at which more effort is put in as the fish population drops while μ is the horizontal shift parameter which places half the maximum effort at the fish population $\frac{\mu}{\lambda}$. As with equation 1.4, more fish cannot be harvested than exist, hence requiring that $q \frac{N + \rho(S)}{1 + e^{(\lambda x - \mu)}} \leq 1 \implies q \leq \frac{1 + e^{(\lambda x - \mu)}}{N + \rho(S)}$.

For each scenario, the decline of the fish population induces stress among the community dependent on the harvest. As fishermen transition through different states of non-stressed, stressed, and recovered, the effort the community puts towards fishing is affected, and in turn, affects further transitions.

1.3.2 Stress Contagion Model

Fishermen can transition between non-stressed (N), stressed (S), and recovered (R) states by either directly observing the fish decline, where fish population is denoted as $x(t)$, or by communicating with other members of the community and choosing to proactively adopt an alternate state based on the interaction. Equations 1.6, 1.7, and 1.8 are combined with specifications of the fish population equations (equations 1.1, 1.2, and 1.3) to create a full ODE system for how fishermen move through the different states. The summation terms are the expectations of

$$\frac{dN}{dt} = \left(\frac{r_3 x}{K} + \sum_{z_N=1}^N \gamma P_N \right) S - \left(\frac{r_1(K-x)}{K} + \sum_{z_S=1}^S \beta P_S + \sum_{z_S=1}^S \delta P_S \right) N \quad (1.6)$$

$$\frac{dS}{dt} = \left(\frac{r_1(K-x)}{K} + \sum_{z_S=1}^S \beta P_S \right) N - \left(\frac{r_2(K-x)}{K} + \frac{r_3 x}{K} + \sum_{z_R=1}^R \psi P_R + \sum_{z_N=1}^N \gamma P_N \right) S \quad (1.7)$$

$$\frac{dR}{dt} = \left(\frac{r_2(K-x)}{K} + \sum_{z_R=1}^R \psi P_R \right) S + \sum_{z_S=1}^S \delta P_S N \quad (1.8)$$

transitioning between states by interacting with people from another state.

Table 1.1 defines parameters that complete the ODE system. Here, r_1 , r_2 , and r_3 are the rates at which fishermen transition between states by directly observing the fish population. The terms in the system involving r_1 , r_2 , and r_3 do not involve any interaction between humans. This allows for all fishermen to start in the non-stressed state and the initial transition to the stressed state occurs from observing the fish population.

The parameters γ , β , δ , and ψ are the effect that a certain number of human interactions have on a person transitioning states. Each of these follows a logistic curve represented below.

$$\begin{aligned}\gamma &= \frac{1}{1 + e^{-(z_N - \alpha_1)/\phi_1}} \\ \beta &= \frac{1}{1 + e^{-(z_S - \alpha_2)/\phi_2}} \\ \psi &= \frac{1}{1 + e^{-(z_R - \alpha_3)/\phi_3}} \\ \delta &= \frac{1}{1 + e^{-(z_S - \alpha_4)/\phi_4}}\end{aligned}$$

Note that α_1 , α_2 , α_3 , α_4 are location parameters that govern how many interactions with people are required to result in a 0.5 chance of changing states. For example, if interactions of 4 people are required for a 0.5 chance of changing states, the α value will be set to 4. ϕ_1 , ϕ_2 , ϕ_3 , and ϕ_4 are scale parameters which affect the spread of influence change between the number of people contacted. The shape of these curves allows us to capture a dynamic in which greater numbers of people contacted collectively have a greater influence on a fisherman changing states.

The terms P_N , P_S , and P_R are the probabilities of coming into contact with a specific number of people of a corresponding state. Each of these terms adopt the Poisson distributions listed below where $0 < c < 1$ is the connectivity of the

Table 1.1: Parameters and terms incorporated into ODE system

r_1	parameter for transmission from non-stressed to stressed
r_2	parameter for transmission from stressed to recovered
r_3	parameter for transmission from stressed to non-stressed
γ	rate of moving from stressed to non-stressed when coming into contact with z_N number of non-stressed people
β	rate of moving from non-stressed to stressed when coming into contact with z_S number of stressed people
δ	rate of moving from non-stressed to recovered when coming into contact with z_S number of stressed people
ψ	rate of moving from stressed to recovered when coming into contact with z_R number of recovered people
$P_N(z_N, N)$	probability of having contact with z_N number of non-stressed people
$P_S(z_S, S)$	probability of having contact with z_S number of stressed people
$P_R(z_R, R)$	probability of having contact with z_R number of recovered people

community and z_i is the number of people in state i that were contacted.

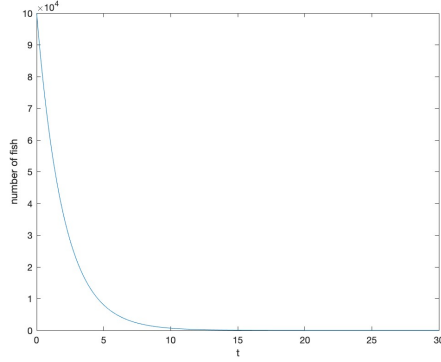
$$\begin{aligned} P_N &= Pois(cN) = \frac{(cN)^{z_N} e^{-cN}}{z_N!} \\ P_S &= Pois(cS) = \frac{(cS)^{z_S} e^{-cS}}{z_S!} \\ P_R &= Pois(cR) = \frac{(cR)^{z_R} e^{-cR}}{z_R!} \end{aligned}$$

For example, if the community is highly connected, there is a higher probability of interacting with exactly 20 people from state i than with exactly 3 people, but if the community is poorly connected, there will be a higher probability of interacting with exactly 3 people from state i than with exactly 20 people. Summing over the parameters γ , β , δ , and ψ and terms P_N , P_S , and P_R gives us the expectation of changing states based on communicating with other community members, creating the complex contagion aspect of the model.

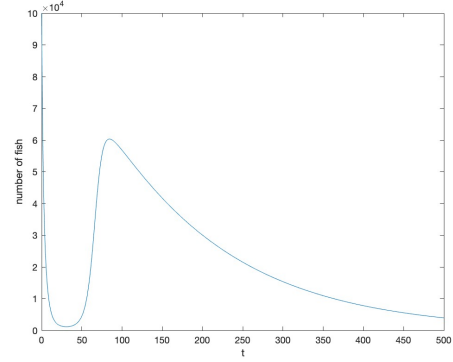
1.4 Analysis

For each scenario, we look at the stability using Jacobian analysis [19]. The Jacobian matrices and further details can be found in the appendix. Stress-free equilibria were found and used in the Jacobian matrix. For all cases, the stress-free equilibria are unstable due to the criteria of having at least one zero eigenvalue [61].

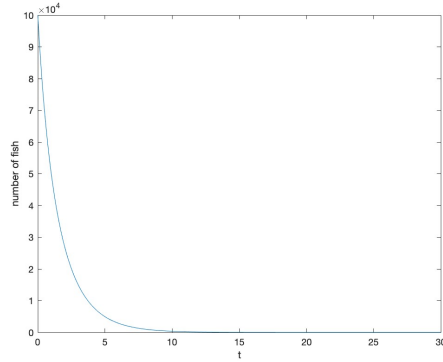
Combining equations 1.1, 1.2, 1.3 with 1.4 and 1.5, we analyze how the fish population reacts under different circumstances. Looking at Figure 1.1, the different specifications of fish population decline are coupled with equation 1.4, which is the fishing effort representing the total fishermen fishing. For comparison, the catchability, initial fish population, and human population are kept the same across all cases. Cases 1.1a and 1.1c have similar shapes, meaning that neither case allows for a temporary population recovery. Interestingly, case 1.1b, does allow for a temporary



(a) Uses equation 1.1 and 1.4 with $K = 150,000$, $r = -0.01$

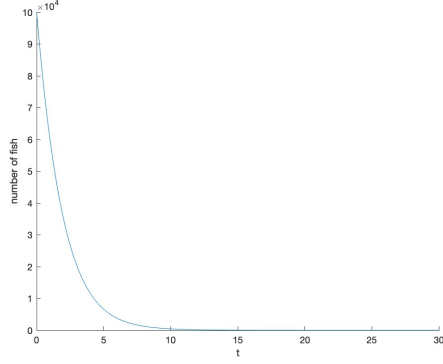


(b) Uses equation 1.2 and 1.4 with $K_0 = 150,000$, $b = 0.007$, and $r = 0.3$

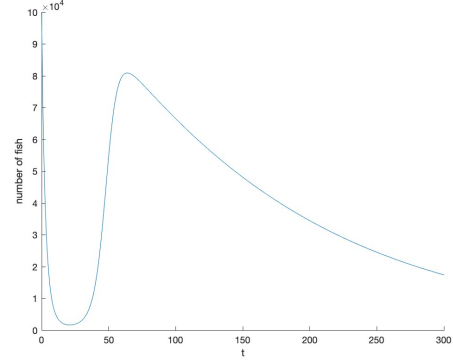


(c) Uses equation 1.3 and 1.4 with $K = 150,000$, $m = 0.35$, and $r = 0.3$

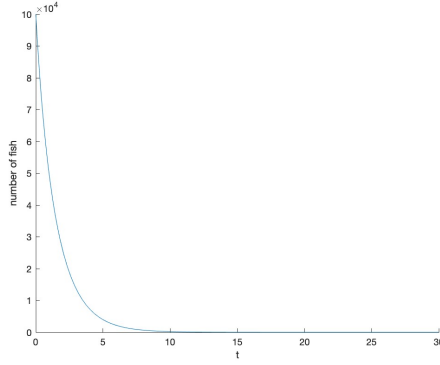
Figure 1.1: The figures above use a $q = 0.001$ (catchability), $x_0 = 100,000$ (initial fish population), and the community population being 500 with all fishermen starting as non-stressed



(a) Uses equation 1.1 and 1.5 with $K = 150,000$, $r = -0.01$



(b) Uses equation 1.2 and 1.5 with $K_0 = 150,000$, $b = 0.007$, and $r = 0.3$



(c) Uses equation 1.3 and 1.5 with $K = 150,000$, $m = 0.35$, and $r = 0.3$

Figure 1.2: The figures above use equation 1.5 as the fishing effort with $\rho = 3$, $\lambda = .07$, and $\mu = x_0/2$, which shifts the curve to center around half of the initial fish population. $q = 0.001$ (catchability), $x_0 = 100,000$ (initial fish population), and the community population is 500, with all fishermen starting as non-stressed. The following are parameters corresponding to 1.5 $\rho = 3$, $\mu = 0.5$, $\lambda = 0.07$.

population recovery due to a large enough difference in the growth rate of the fish and the harvest rate. However, as the carrying capacity shrinks, the difference shrinks, limiting the duration of the effect and resulting in only a temporary recovery in the fish population. Figure 1.2 has similar shapes as Figure 1.1 indicating that when stressed fishermen put in more effort as the fish population drops (equation 1.5), the fish population decline follows similar trajectories as when both non-stressed and stressed fishermen put in the same effort (equation 1.4).

For further analysis of how different combinations and certain parameters affect the system, we break the non-stressed class into two subclasses: non-stressed that has never been stressed, and non-stressed that has moved into the stressed class and then moved back to the non-stressed class at least once. This allows us to track the number of people who were never stressed and moved into the recovered class due to social interaction with stressed people and subsequent proactive avoidance of the stressed state. Doing that results in the following modification to the equations 1.6, 1.7, and 1.8 where N_1 is non-stressed people who have never been stressed and N_2 is non-stressed people who have been stressed.

$$\frac{dN_1}{dt} = - \left(\frac{r_1(K-x)}{K} + \sum_{z_S=1}^S \beta P_S + \sum_{z_S=1}^S \delta P_S \right) N_1 \quad (1.9)$$

$$\frac{dN_2}{dt} = \left(\frac{r_3x}{K} + \sum_{z_N=1}^{N_1+N_2} \gamma P_{N_1+N_2} \right) S - \left(\frac{r_1(K-x)}{K} + \sum_{z_S=1}^S \beta P_S + \sum_{z_S=1}^S \delta P_S \right) N_2 \quad (1.10)$$

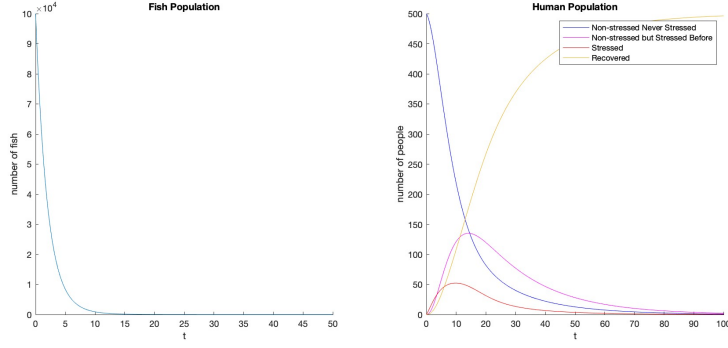
$$\begin{aligned} \frac{dS}{dt} = & \left(\frac{r_1(K-x)}{K} + \sum_{z_S=1}^S \beta P_S \right) (N_1 + N_2) \\ & - \left(\frac{r_2(K-x)}{K} + \frac{r_3x}{K} + \sum_{z_R=1}^R \psi P_R + \sum_{z_N=1}^{N_1+N_2} \gamma P_{N_1+N_2} \right) S \end{aligned} \quad (1.11)$$

$$\frac{dR}{dt} = \left(\frac{r_2(K-x)}{K} + \sum_{z_R=1}^R \psi P_R \right) S + \sum_{z_S=1}^S \delta P_S (N_1 + N_2) \quad (1.12)$$

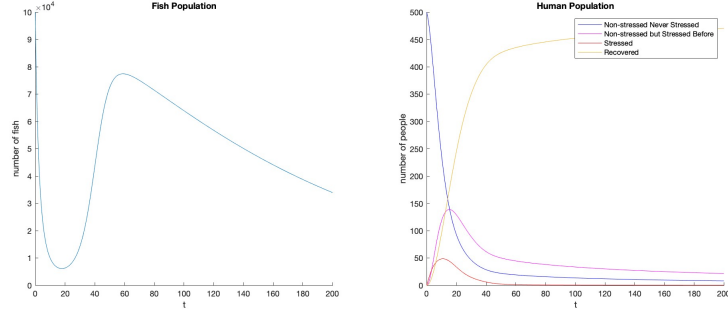
First, we examine how the different fish population decline scenarios, coupled with the different fishing effort scenarios, affect the total number of people that become stressed, the peak number of people stressed simultaneously, the average time a person is stressed, and the event duration (that is, the time it takes for everyone in the community to move into the recovered class from the initial stress case). Event duration is a unitless time variable used for comparison throughout the analysis. Figures 1.3 and 1.4 go through the different scenarios. We find that the different effort scenarios (whether stressed people behave differently) overall did not have a large impact. The most noticeable impact occurred in an event duration difference of 7.3887 between 1.3b and 1.4b with 1.4b being the lowest. The time spent stressed, the total number of people that became stressed, and the peak number stressed were all comparable, with the peak number stressed having the most variation.

Next we will look at how the connectivity of the community affects how stress moves through the population. Figure 1.5 compares different values of connectivity across all cases using the same parameters as in figures 1.3 and 1.4. Precise numbers are found in the captions of figures 1.8- 1.13, which are found in the appendix.

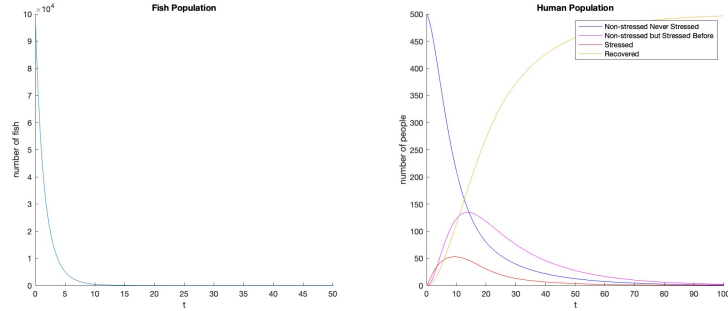
An increase in connectivity across all cases leads to a shorter event time, with fewer people spending time in the stressed state. Also, more people were able to avoid the stressed state completely and skip straight to the recovered state through social interactions leading to informed, proactive decisions. However, this comes at the cost of an increased peak number of people stressed at one time.



(a) Uses equation 1.1 and 1.4 with $K = 150,000$, $r = -0.01$ for the fishing scenario. The average time a person stressed is about 1.5 years, the duration of the event is 74 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 52 .

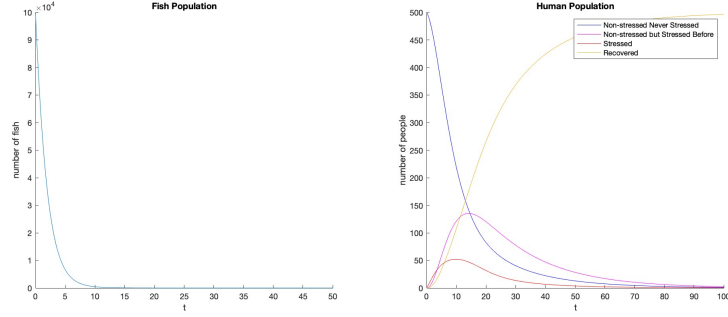


(b) Uses equation 1.2 and 1.4 with $K_0 = 150,000$, $b = 0.007$, and $r = 0.3$. The average time a person stressed is about 1.5 years, the duration of the event is 65 years, the total number of people that become stressed is ~ 396 , and the peak number of stressed people is ~ 49 .

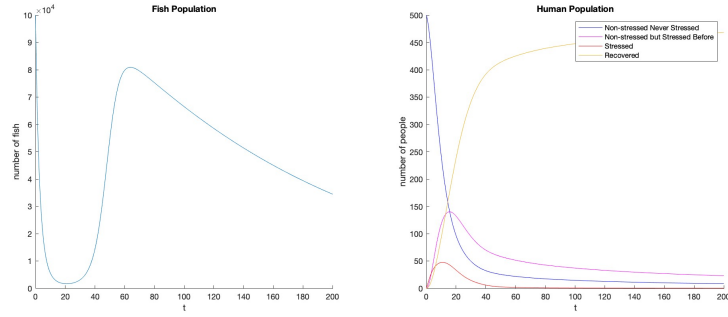


(c) Uses equation 1.3 and 1.4 with $K = 150,000$, $m = 0.35$, and $r = 0.3$. The average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 53 .

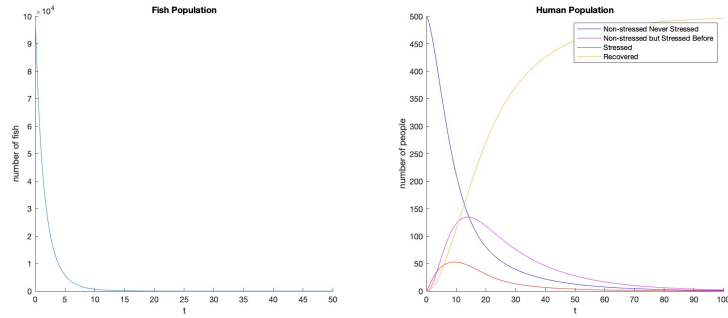
Figure 1.3: The figures use equation 1.4 as the fishing effort along with $q = 0.001$ (catchability), $x_0 = 100,000$ (initial fish population), and a community population of 500, in which all people start in the N_1 class. Also, $c = 0.01$ (community connectivity), $\alpha = 4$, $\phi = 1$, and $r_1 = r_2 = r_3 = 0.05$ are used across cases.



(a) Uses equation 1.1 and 1.5 with $K = 150,000$, $r = -0.01$ for the fishing scenario. The average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 393 , and the peak number of stressed people is ~ 53 .



(b) Uses equation 1.2 and 1.5 with $K_0 = 150,000$, $b = 0.007$, and $r = 0.3$. The average time a person stressed is about 1.5 years, the duration of the event is 58 years, the total number of people that become stressed is ~ 396 , and the peak number of stressed people is ~ 50 .



(c) Uses equation 1.3 and 1.5 with $K = 150,000$, $m = 0.35$, and $r = 0.3$. The average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 53 .

Figure 1.4: The figures use equation 1.5 as the fishing effort with $\rho = 3$, $\lambda = .07$, and $\mu = x_0/2$ which shifts curve to center around half of the initial fish population. $q = 0.001$ (catchability), $x_0 = 100,000$ (the initial fish population), and the community population is 500, with all people starting in the N_1 class. Also, $c = 0.01$ (community connectivity), $\alpha = 4$, $\phi = 1$, and $r_1 = r_2 = r_3 = 0.05$ are used across cases.

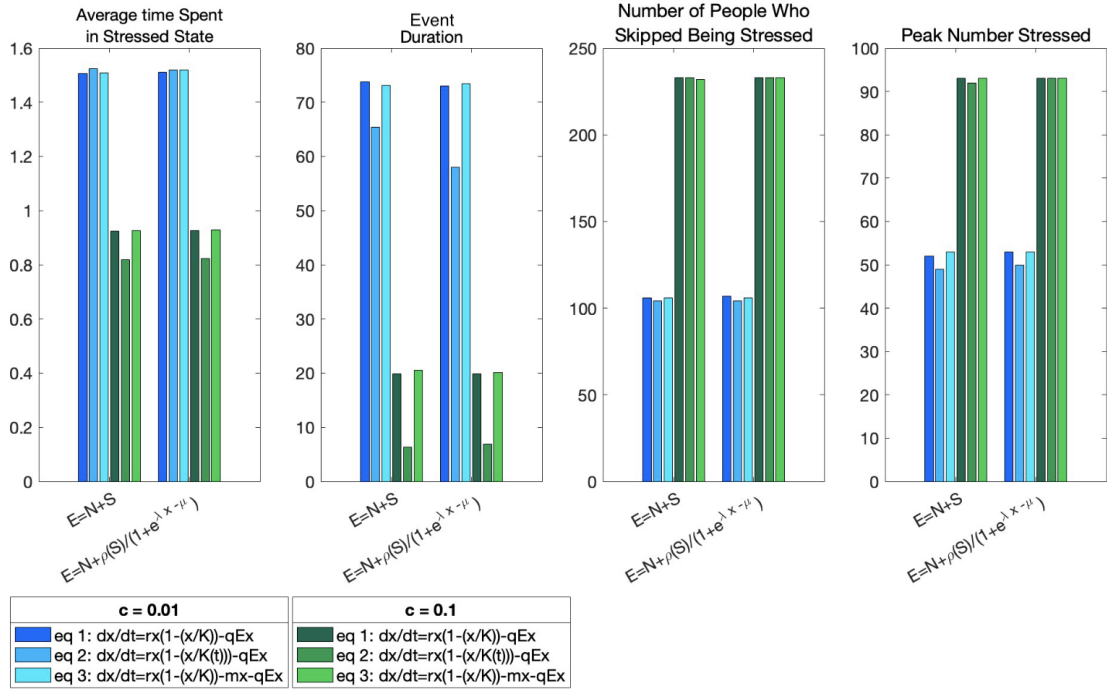


Figure 1.5: Compares a connectivity value of 0.01 with a connectivity value of 0.1 across equations 1.1, 1.2, and 1.3, while also considering the different effort functions 1.4 and 1.5. In a more connected community, both the average time a person spends in the stressed state and the total event duration decrease, while both the number of people able to skip the stressed state and the peak number of people stressed at a given time increase.

1.5 Discussion

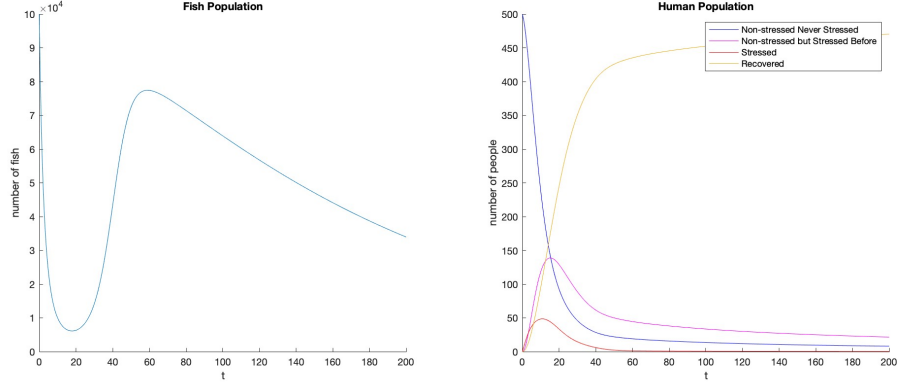
This paper presents a novel model that can help understand and predict the dynamics of a community facing the disappearance of their main source of income as they transition to a new income source, and how stress and social support may play a role in that transition. We examine different scenarios of species decline and its impacts on a community dependent on harvest; explore the impact of conservation efforts on the duration of the transition event and the peak number of simultaneously stressed individuals; and provide insight into how the connectivity of a community may affect an individual's transition to a new income source.

We considered several different scenarios that could cause inevitable species decline, the most applicable being habitat loss and proportional removal, such as due to disease. Habitat loss has happened in several cases throughout history and is still happening currently. In the California Current System (CCS), habitat loss is occurring due to intensifying hypoxia, which is when oxygen drops to inefficient levels [54]. This has been found to affect species distribution as it makes previous habitable regions or depths uninhabitable [54]. Sawfish are also severely threatened due to a combination of overfishing and habitat loss. Habitat loss occurs directly through avenues such as commercial development, residential development, and modifications to natural systems, and overfishing amplifies the issue [122]. Both of these sources show how the future of a species may be impacted due to human activity directly or indirectly shrinking the species' habitat. Disease is another complication that can cause population collapse. Amphibian chytridiomycosis has caused species decline and even extinction in several cases [11]. And although species-dependent management suggestions are given, some species might not survive without intervention [11]. Clearly, species decline can be driven by several different factors. In our research, we analyze how these situations affect how humans might experience an income transition if conservation efforts focusing on reversing the underlying (fishing-independent) drivers of population decrease are either not implemented or not successful. Using

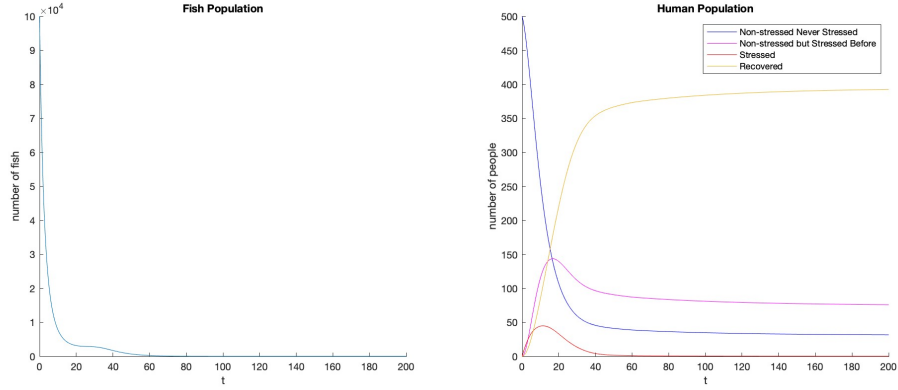
figures 1.1 and 1.2, we can see that the species population decline varies across scenarios with habitat loss, allowing for a temporary partial recovery of the species. Figures 1.3 and 1.4 show that the reason for species decline does not severely alter the transition humans take to reach the recovered state. However, habitat loss does lead to a shorter event duration. Also, a fishing effort in which stressed fishermen put in more effort leads to a shorter event duration than if all fishermen consistently undertake the same effort. This reinforces statements made in [122] that habitat loss repercussions can be amplified by fishing efforts. Increased stress and desperation resulting in increased fishing effort can have negative effects on people’s health, for example by experiencing anxiety, diminished cognitive functions (such as ability to focus), and behavioral issues such as sleep disruption and clumsiness [78]. It is important to consider the effects different decline scenarios present, along with the potential behavioral changes of fishermen, to adequately predict and prepare for a community loss of income.

We also considered how conservation efforts affect community members’ transition through stress states. Note that in cases relevant to this paper, true species conservation is not attainable, but conservation efforts could delay time to extinction or near extinction. However, conservation can be an expensive endeavour both economically and socially [83]. Therefore, any benefit that conservation would have on the community’s mental health would have to be worth the costs. Figure 1.6 shows that if conservation efforts are used to change habitat degradation to a level of $b = 0.007$ from a level of $b = 0.1$, the number of people able to skip stressed state stayed the same while the peak number of stressed people went up by 4. The duration of the event dropped from 65 to 61 years, but the time a person spent stressed remained comparable. This reveals that conservation efforts that decrease the rate of habitat loss could make the transition event duration longer, preventing people from proactively avoiding becoming stressed.

Figure 1.7 reveals how conservation efforts made towards preserving a species that has proportional removals affects a community. In the case in which a removal rate of

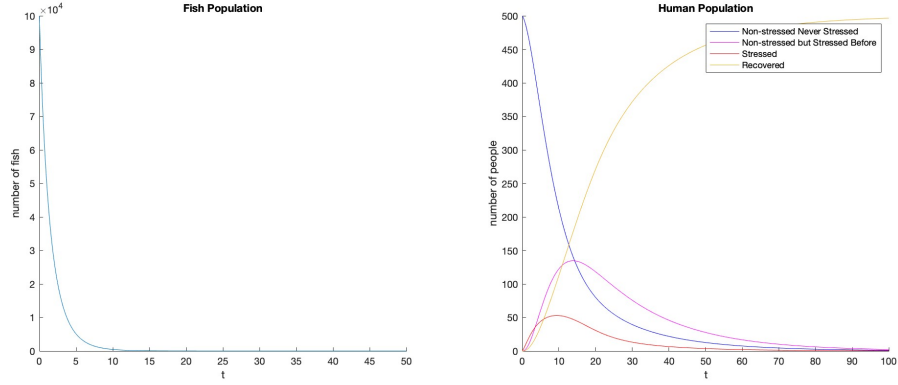


(a) All parameter values are as in figure 1.3b, except for the rate of habitat decline, which is here $b = 0.007$.

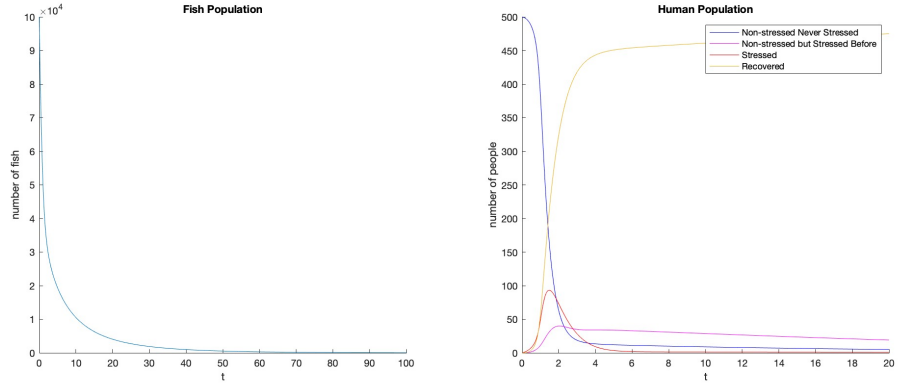


(b) All parameters are as in 1.6a with a change in habitat degradation rate to $b = 0.1$. The average time a person stressed is about 2 years, the duration of the event is 61 years, the total number of people that become stressed is ~ 396 , and the peak number of stressed people is ~ 45 . The number of people that skipped the stressed state is ~ 104 .

Figure 1.6: Compares how different rates of habitat degradation affects human transition with the case combination of equation 1.2 and 1.4.



(a) All parameters are as in figure 1.3c, excepting the proportional removal, which here is $m = 0.35$.



(b) Uses the same parameters as 1.7a, except for a change in proportional removal to $m = 0.8$. The average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 393 , and the peak number of stressed people is ~ 54 . The number of people that skipped the stressed state is ~ 107 .

Figure 1.7: Compares how different values of proportional removal affects human transitions with the case combination of equation 1.3 and 1.4.

$m = 0.8$ is brought down to $m = 0.35$, the peak number of stressed people decreased by 1, but the number of people that skipped the stressed state dropped by 1. The time a person spent being stressed and the duration of the event were comparable. Again, in this case, conservation efforts might not be economically worthwhile due to being able to achieve only minor differences in overall outcomes. However, this may change under different scenarios which would alter model parametrization or functional forms.

The model presented in this paper can aid in vital conservation policy decisions and help reduce expenditures on fruitless conservation efforts.

Lastly, we find that the connectivity of a community can impact how a community transitions. Figure 1.5 shows how an increase in connectivity values of a community can lead to an increase in the peak number of stressed individuals, but provides a decrease in both the time a person spends stressed and the overall event duration. Also, significantly more people were able to skip over the stressed state due to higher connectivity in the community. A more connected community can therefore have a profound impact on population-wide mental health outcomes, with the biggest impacts deriving from the increase in people leveraging socially derived support and information about their options to either avoid stress entirely or, at least, decrease their time spent being stressed. The literature supports that community connectedness and mental health are intertwined. Particularly, [100] looks at how connectivity affects mental health and vice versa. It is found that connectedness and mental health are positively and reciprocally associated. However, connectedness is a stronger indicator of mental health than mental health is for connectivity. This reinforces the importance of connecting the community to improve mental health even in the face of crisis.

Several methods can be used to increase the connectivity of a community. [27] suggests to improve community connectivity and sense of community, neighborhoods could be required to apply for government assistance as a group instead of individually, and support could be given to the development of neighborhood group organizations,

such as a crime watch, which can foster a sense of shared values and goals, leading to increased interpersonal support. Additionally, [95] presented the creation of a public center or “community house” in New Zealand in which community events such as crafts, hobbies, child care, local movies, etc., were held to foster fulfilling shared community experience. Government agencies might choose to implement similar tactics for increasing connectivity to reduce the stress of an inevitable transition as natural resources become unsustainable sources of community income.

1.6 Current Limitations and Future Work

Although our paper provides valuable additions to community mental health, there are some limitations to keep in mind. For instance, what is considered the best option accounting for both mental health and economic budgets is not easily answered. Therefore, although our model provides clear comparisons among scenarios, we do not suggest a clear plan of action. Government agencies and policymakers should consider scenario-specific factors to devise an appropriate plan of action with explicit consideration of questions such as “Is it better for the mental health of the community to be more connected and transition more quickly, but at the expense of a higher peak total in simultaneously stressed individuals, or to ‘flatten the curve’ and transition over a longer period, but ensure that only relatively few individuals are stressed at any one time”?

Extensions can also be made to include more nuanced economic, sociological, and psychological components. Currently, the financial impact on an individual is not considered past the stress it might induce. Similarly, other factors such as family history, age, education, and economic status are not considered. However, factors such as these may affect a fisherman’s choice to continue fishing and incorporating them could add additional insight [31]. For example, having a lineage of fishermen, the time spent as a fisherman, or the years lived in the fishing community could potentially change the decision a person makes to leave the career. Another extension

could be to allow departure and entrance into the community. A requirement such as a fishing license, fees, or other documentation might regulate the incoming population by requiring cost analysis by the individual to determine if the upfront cost of joining would be outweighed by the payout once joined. The departing population would have to weigh the cost of leaving the community, such as fees for breaking a contract or moving costs to determine if the new income source would make up for the financial loss upfront. Also, the connectedness of the community could affect the decision to leave. If the community is highly connected, members might be less likely to leave due to a sense of belonging. Additionally, allowing migration could lead to the complete abandonment of the community, or the creation of a ghost town, as the livelihood of the community is put in jeopardy.

The work presented focuses on a fishing community and reveals how ecological, economic, and social factors impact how a community can expect to be affected by stress. However, the methods presented here can be extended to many other scenarios. For example, the U.S. coal industry has been in decline due to rising coal prices, mechanization of coal mining, and environmental regulations [17]. Additionally, areas rich in coal resources are unlikely to have a diverse job market due to people forgoing advanced education for the preference of tapping into the highly unionized, high-paying jobs of the coal industry [17]. This puts excess strain on coal communities to adapt and transition. Implementation of the methods found in this paper could help to plan and assist coal communities by answering questions such as how the decline trajectory would likely affect the income transition. Additionally, increasing the connectivity of the community could influence members to proactively forgo the coal industry completely or transition to a different career path before they reach financial devastation. In addition to the coal industry, the print newspaper industry is facing collapse due to an increase in the digital world, putting stress on their current business model [60]. Although it is less likely to find entire communities reliant for their economic well-being solely on the production of print media, nonetheless, the insights from these models apply to a socially (rather than spatially) united

community of journalists and publishers. The methods in this paper shed light on the potential timeline and mental repercussions the transition to a different business model may induce. There are several other cases where the methods in this model could provide insightful information.

1.7 Conclusion

Here, we have presented a complex contagion model to explore the stress-related mental health dynamics of a community dependent on a declining industry. We focused our model on the case study of a fishing community whose harvest species is on a trajectory to (near)extinction. We explored ecological, economic, and socio-psychological factors to understand how best to support a community in transition away from reliance on an inevitably diminishing resource. This work complements the existing literature that has traditionally focused more on exploring the coupled dynamics of exploitation and sustainability in resource management. We expect these results to be especially valuable for consideration of communities relying on resources that are diminishing not solely as a result of their own practices or factors that are wholly under their own control. Our model serves both to highlight how we might begin to study such populations and how we might best inform policies to support communities facing these circumstances. A diversity of industries, and the communities that rely on them, face demise from inevitably exhausted resources. By improving support to populations whose communal livelihoods are threatened, we may be able not only to avoid negative mental health, physical health, and socioeconomic impacts in the near term but may be able to avoid generational impacts on wealth and well-being for entire communities.

1.8 Acknowledgments

We appreciate Dr. Justin Wright's help with the early implementation of the code.

Appendix

Here, we provide the stability analysis of the different equation combinations. Note that for taking the derivative of summation terms, a difference operator was used if the variable we were differentiating with respect to was the upperbound. Otherwise, the summation is a constant based on the other state levels.

1. $\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - qEx$ with $E = N + S$ (Equations 1.1 and 1.4)

$$J = \begin{bmatrix} r - 2\frac{rx}{K} - q(N + S) & -qx & & & & \\ \frac{r_3S}{K} + \frac{r_1N}{K} & \frac{SP_N(N,N)}{1+e^{-(N-\alpha_1)/\phi_1}} - r_1 + \frac{r_1x}{K} - \sum_{z=1}^S \beta P_S - \sum_{z=1}^S \delta P_S & & & & \\ -\frac{r_1N}{K} + \frac{r_2S}{K} - \frac{r_3S}{K} & r_1 - \frac{r_1x}{K} + \sum_{z=1}^S \beta P_S - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} & & & & \\ -\frac{r_2S}{K} & & \sum_{z=1}^S \delta P_S & & & \\ & -qx & & & 0 & \\ \frac{r_3x}{K} + \sum_{z=1}^N \gamma P_N - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & & & 0 & \\ \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - r_2 + \frac{r_2x}{K} - \frac{r_3x}{K} - \sum_{z=1}^R \psi P_R - \sum_{z=1}^N \gamma P_N & & & -\frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & & \\ r_2 - \frac{r_2x}{K} + \sum_{z=1}^R \psi P_R + \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & & \frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & & \end{bmatrix}$$

Stress-free equilibrium: $(x, N, S, R) = (K, 0, 0, A)$, $(0, 0, 0, A)$ where $A = N + R + S$ is the total human population.

Jacobian at $(K, 0, 0, A)$:

$$J(K, 0, 0, A) - I\lambda = \begin{bmatrix} -r - \lambda & -qK & -qK & 0 \\ 0 & -\lambda & r_3 & 0 \\ 0 & 0 & -r_3 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

Taking the determinant and setting is equal to zero gets you:

$$\lambda^2 \left(rr_3 + r \sum_{z=1}^A \psi P_R + \lambda(r + r_3 + \sum_{z=1}^A \psi P_R) + \lambda^2 \right) = 0$$

which gives the following eigenvalues:

$$\lambda_1, \lambda_2 = 0$$

$$\lambda_3 = \frac{1}{2} \left[\left(r + r_3 + \sum_{z=1}^A \psi P_R \right) + \sqrt{\left(r + r_3 + \sum_{z=1}^A \psi P_R \right)^2 - 4 \left(rr_3 + r \sum_{z=1}^A \psi P_R \right)} \right]$$

$$\lambda_4 = \frac{1}{2} \left[\left(r + r_3 + \sum_{z=1}^A \psi P_R \right) - \sqrt{\left(r + r_3 + \sum_{z=1}^A \psi P_R \right)^2 - 4 \left(rr_3 + r \sum_{z=1}^A \psi P_R \right)} \right]$$

Since we have zero eigenvalues, the equilibrium is **unstable**.

Jacobian at $(0, 0, 0, A)$:

$$J(0, 0, 0, A) - I\lambda = \begin{bmatrix} r - \lambda & 0 & 0 & 0 \\ 0 & -r_1 - \lambda & 0 & 0 \\ 0 & r_1 & -r_2 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2 + \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

$$\lambda_1 = r, \lambda_2 = -r_1$$

$$\lambda_3 = -r_2 - \sum_{z=1}^A \psi P_R, \lambda_4 = 0$$

Since we have zero eigenvalues, the equilibrium is **unstable**.

$$2. \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - qEx \text{ with } E = N + \frac{\rho(S)}{1+e^{(\lambda x - \mu)}} \text{ (Equations 1.1 and 1.5)}$$

$$J = \begin{bmatrix} r - 2\frac{rx}{K} - qN + q\rho(S) \frac{(1+e^{\lambda^* x - \mu}) + \lambda^* x e^{\lambda^* x - \mu}}{(1+e^{\lambda^* x - \mu})^2} & \frac{-qx}{1+e^{\lambda^* x - \mu}} & & & \\ \frac{r_3 S}{K} + \frac{r_1 N}{K} & \frac{SP_N(N, N)}{1+e^{-(N-\alpha_1)/\phi_1}} - r_1 + \frac{r_1 x}{K} - \sum_{z=1}^S \beta P_S - \sum_{z=1}^S \delta P_S & & & \\ -\frac{r_1 N}{K} + \frac{r_2 S}{K} - \frac{r_3 S}{K} & r_1 - \frac{r_1 x}{K} + \sum_{z=1}^S \beta P_S - \frac{NP_S(S, S)}{1+e^{-(S-\alpha_2)/\phi_2}} & & & \\ -\frac{r_2 S}{K} & \sum_{z=1}^S \delta P_S & & & \\ & \frac{q\rho x}{1+e^{\lambda^* x - \mu}} & & & 0 \\ & \frac{r_3 x}{K} + \sum_{z=1}^N \gamma P_N - \frac{NP_S(S, S)}{1+e^{-(S-\alpha_2)/\phi_2}} - \frac{NP_S(S, S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & & 0 \\ & \frac{NP_S(S, S)}{1+e^{-(S-\alpha_2)/\phi_2}} - r_2 + \frac{r_2 x}{K} - \frac{r_3 x}{K} - \sum_{z=1}^R \psi P_R - \sum_{z=1}^N \gamma P_N & & & -\frac{SP_R(R, R)}{1+e^{-(R-\alpha_3)/\phi_3}} \\ & r_2 - \frac{r_2 x}{K} + \sum_{z=1}^R \psi P_R + \frac{NP_S(S, S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & & \frac{SP_R(R, R)}{1+e^{-(R-\alpha_3)/\phi_3}} \end{bmatrix}$$

Stress-free equilibrium: $(x, N, S, R) = (K, 0, 0, A)$, $(0, 0, 0, A)$ where $A = N + R + S$ is the total human population.

Jacobian at $(K, 0, 0, A)$:

$$J(K, 0, 0, A) - I\lambda = \begin{bmatrix} -r - \lambda & -qK & -qK & 0 \\ 0 & -\lambda & r_3 & 0 \\ 0 & 0 & -r_3 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

Taking the determinant and setting it equal to zero gets you:

$$\lambda^2 \left(rr_3 + r \sum_{z=1}^A \psi P_R + \lambda(r + r_3 + \sum_{z=1}^A \psi P_R) + \lambda^2 \right) = 0$$

which gives the following eigenvalues:

$$\lambda_1, \lambda_2 = 0$$

$$\lambda_3 = \frac{1}{2} \left[\left(r + r_3 + \sum_{z=1}^A \psi P_R \right) + \sqrt{\left(r + r_3 + \sum_{z=1}^A \psi P_R \right)^2 - 4 \left(rr_3 + r \sum_{z=1}^A \psi P_R \right)} \right]$$

$$\lambda_4 = \frac{1}{2} \left[\left(r + r_3 + \sum_{z=1}^A \psi P_R \right) - \sqrt{\left(r + r_3 + \sum_{z=1}^A \psi P_R \right)^2 - 4 \left(rr_3 + r \sum_{z=1}^A \psi P_R \right)} \right]$$

Since we have zero eigenvalues, the equilibrium is **unstable**.

Jacobian at $(0, 0, 0, A)$:

$$J(0, 0, 0, A) - I\lambda = \begin{bmatrix} r - \lambda & 0 & 0 & 0 \\ 0 & -r_1 - \lambda & 0 & 0 \\ 0 & r_1 & -r_2 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2 + \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

$$\lambda_1 = r, \lambda_2 = -r_1$$

$$\lambda_3 = -r_2 - \sum_{z=1}^A \psi P_R, \lambda_4 = 0$$

Since we have zero eigenvalues, the equilibrium is **unstable**.

3. $\frac{dx}{dt} = rx \left(1 - \frac{x}{K(t)}\right) - qEx$ with $E = N + S$ (Equations 1.2 and 1.4)

Same as the corresponding previous case

4. $E = \frac{\rho(N+S)}{1+e^{(\lambda x - \mu)}}$ (Equations 1.2 and 1.5)

Same as the corresponding previous case

5. $\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - mx - qEx$ with $E = N + S$ (Equations 1.3 and 1.4)

$$J = \begin{bmatrix} r - 2\frac{rx}{K} - m - q(N+S) & -qx & & & & \\ & \frac{r_3S}{K} + \frac{r_1N}{K} & \frac{SP_N(N,N)}{1+e^{-(N-\alpha_1)/\phi_1}} - r_1 + \frac{r_1x}{K} - \sum_{z=1}^S \beta P_S - \sum_{z=1}^S \delta P_S & & & \\ & -\frac{r_1N}{K} + \frac{r_2S}{K} - \frac{r_3S}{K} & r_1 - \frac{r_1x}{K} + \sum_{z=1}^S \beta P_S - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} & & & \\ & -\frac{r_2S}{K} & \sum_{z=1}^S \delta P_S & & & \\ & & & -qx & & 0 \\ & & & \frac{r_3x}{K} + \sum_{z=1}^N \gamma P_N - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & 0 \\ & & & \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - r_2 + \frac{r_2x}{K} - \frac{r_3x}{K} - \sum_{z=1}^R \psi P_R - \sum_{z=1}^N \gamma P_N & -\frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & \\ & & & r_2 - \frac{r_2x}{K} + \sum_{z=1}^R \psi P_R + \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & \frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & \end{bmatrix}$$

Stress-free equilibria: $(x, N, S, R) = (0, 0, 0, A)$, $\left(\frac{K(r-m)}{r}, 0, 0, A\right)$, $\left(K, -\frac{m}{q}, 0, A + \frac{m}{q}\right)$ where $A = N + R + S$. Notice the equilibrium $\left(K, -\frac{m}{q}, 0, A + \frac{m}{q}\right)$ is not possible since $N < 0$. is the total human population

Jacobian at $(0, 0, 0, A)$:

$$J(0, 0, 0, A) - I\lambda = \begin{bmatrix} -r - m - \lambda & 0 & 0 & 0 \\ 0 & -r_1 - \lambda & 0 & 0 \\ 0 & r_1 & -r_2 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2 - \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

$$\lambda_1 = r - m, \lambda_2 = -r - 1, \lambda_3 = -r_2 - \sum_{z=1}^A \psi P_R, \lambda_4 = 0$$

Since we have a zero eigenvalue, the equilibrium is **unstable**.

Jacobian at $\left(\frac{K(r-m)}{r}, 0, 0, A\right)$:

$$J\left(\frac{K(r-m)}{r}, 0, 0, A\right) - I\lambda = \begin{bmatrix} m - r - \lambda & -\frac{qK(r-m)}{r} & \frac{qK(r-m)}{r} & 0 \\ 0 & -r_1 + r_1(r-m) - \lambda & r_3(r-m) & 0 \\ 0 & r_1 - r_1(r-m) & -r_2 + r_2(r-m) - r_3(r-m) - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2 - r_2(r-m) + \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues: After finding the determinant and setting equal to zero, we get

$$\begin{aligned}
& \lambda \left[\lambda^3 + \left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right) \lambda^2 \right. \\
& \quad + \left(m \sum_{z=1}^A \psi P_R - mr_1 \sum_{z=1}^A \psi P_R - r \sum_{z=1}^A \psi P_R + rr_1 \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R \right. \\
& \quad - m^2 r_1 + m^2 r_1 r_2 - m^2 r_2 + m^2 r_3 + 2mrr_1 - 2mrr_1 r_2 + 2mrr_2 - 2mrr_3 - mr_1 \\
& \quad \left. + 2mr_1 r_2 - mr_3 - r^2 r_1 + r^2 r_1 r_2 - r^2 r_2 + r^2 r_3 + rr_1 - 2rr_1 r_2 + rr_2 + r_1 r_2 \right) \lambda \\
& \quad + \left(m^2 r_1 \sum_{z=1}^A \psi P_R - 2mrr_1 \sum_{z=1}^A \psi P_R + mr_1 \sum_{z=1}^A \psi P_R + r^2 r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R - m^3 r_1 r_2 \right. \\
& \quad \left. + 3m^2 rr_1 r_2 - 2m^2 r_1 r_2 - 3mr^2 r_1 r_2 + 4mrr_1 r_2 - mr_1 r_2 + r^3 r_1 r_2 - 2r^2 r_1 r_2 + rr_1 r_2 \right) \Big] = 0
\end{aligned}$$

Using The cubic formula for finding the roots of a cubic polynomial, able to arrive at the following nonzero eigenvalues (Note we have one $\lambda = 0$ eigenvalue):

$$\begin{aligned}
\Delta_0 &= b^2 - 3ac \\
&= \left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right)^2 \\
&\quad - 3 \left(m \sum_{z=1}^A \psi P_R - mr_1 \sum_{z=1}^A \psi P_R - r \sum_{z=1}^A \psi P_R + rr_1 \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R \right. \\
&\quad - m^2 r_1 + m^2 r_1 r_2 - m^2 r_2 + m^2 r_3 + 2mrr_1 - 2mrr_1 r_2 + 2mrr_2 - 2mrr_3 \\
&\quad \left. - mr_1 + 2mr_1 r_2 - mr_3 - r^2 r_1 + r^2 r_1 r_2 - r^2 r_2 + r^2 r_3 + rr_1 - 2rr_1 r_2 + rr_2 + r_1 r_2 \right)
\end{aligned}$$

$$\begin{aligned}
\Delta_1 &= 2b^3 - 9abc + 27a^2d \\
&= 2 \left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right)^3 \\
&\quad - 9 \left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right) \\
&\quad \left(m \sum_{z=1}^A \psi P_R - mr_1 \sum_{z=1}^A \psi P_R - r \sum_{z=1}^A \psi P_R + rr_1 \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R \right. \\
&\quad \left. - m^2 r_1 + m^2 r_1 r_2 - m^2 r_2 + m^2 r_3 + 2mrr_1 - 2mrr_1 r_2 + 2mrr_2 - 2mrr_3 \right. \\
&\quad \left. - mr_1 + 2mr_1 r_2 - mr_3 - r^2 r_1 + r^2 r_1 r_2 - r^2 r_2 + r^2 r_3 + rr_1 - 2rr_1 r_2 + rr_2 + r_1 r_2 \right) \\
&\quad + 27 \left(m^2 r_1 \sum_{z=1}^A \psi P_R - 2mrr_1 \sum_{z=1}^A \psi P_R + mr_1 \sum_{z=1}^A \psi P_R + r^2 r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R - m^3 r_1 r_2 \right. \\
&\quad \left. + 3m^2 rr_1 r_2 - 2m^2 r_1 r_2 - 3mr^2 r_1 r_2 + 4mrr_1 r_2 - mr_1 r_2 + r^3 r_1 r_2 - 2r^2 r_1 r_2 + rr_1 r_2 \right)
\end{aligned}$$

$$C = \sqrt[3]{\frac{\Delta_1 \pm \sqrt{\Delta_1^2 - 4\Delta_0^3}}{2}}$$

$$\begin{aligned}
\lambda_i &= -\frac{1}{3a} \left[b + \xi^i C + \frac{\Delta_0}{\xi^i C} \right] \text{ where } \xi = \frac{-1 + \sqrt{-3}}{2} \\
\lambda_0 &= -\frac{1}{3} \left[\left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right) \right. \\
&\quad \left. + C + \frac{\Delta_0}{C} \right] \\
\lambda_1 &= -\frac{1}{3} \left[\left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right) \right. \\
&\quad \left. + \frac{-1 + \sqrt{-3}}{2} C + \frac{\Delta_0}{\frac{-1 + \sqrt{-3}}{2} C} \right] \\
\lambda_2 &= -\frac{1}{3} \left[\left(mr_1 - m - \sum_{z=1}^A \psi P_R + mr_2 - mr_3 + r - rr_1 - rr_2 + rr_3 + r_1 + r_2 \right) \right. \\
&\quad \left. + \frac{-1 - \sqrt{-3}}{2} C + \frac{\Delta_0}{\frac{-1 - \sqrt{-3}}{2} C} \right]
\end{aligned}$$

Since we know we have at least one zero eigenvalue, the equilibrium is **unstable**.

6. $\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - mx - qEx$ with $E = N + \frac{\rho(S)}{1+e^{(\lambda x - \mu)}}$ (Equations 1.3 and 1.5)

$$J = \begin{bmatrix} r - 2\frac{rx}{K} - m - qN + q\rho(S)\frac{1+e^{\lambda^*x-\mu}-\lambda^*xe^{\lambda^*x-\mu}}{(1+e^{\lambda^*x-\mu})^2} & \frac{-qx}{1+e^{\lambda^*x-\mu}} & & & \\ & \frac{r_3S}{K} + \frac{r_1N}{K} & \frac{SP_N(N,N)}{1+e^{-(N-\alpha_1)/\phi_1}} - r_1 + \frac{r_1x}{K} - \sum_{z=1}^S \beta P_S - \sum_{z=1}^S \delta P_S & & \\ & -\frac{r_1N}{K} + \frac{r_2S}{K} - \frac{r_3S}{K} & r_1 - \frac{r_1x}{K} + \sum_{z=1}^S \beta P_S - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} & & \\ & -\frac{r_2S}{K} & \sum_{z=1}^S \delta P_S & & \\ & & & \frac{q\rho x}{1+e^{\lambda^*x-\mu}} & 0 \\ & & \frac{r_3x}{K} + \sum_{z=1}^N \gamma P_N - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & & 0 \\ & & \frac{NP_S(S,S)}{1+e^{-(S-\alpha_2)/\phi_2}} - r_2 + \frac{r_2x}{K} - \frac{r_3x}{K} - \sum_{z=1}^R \psi P_R - \sum_{z=1}^N \gamma P_N & -\frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & \\ & & r_2 - \frac{r_2x}{K} + \sum_{z=1}^R \psi P_R + \frac{NP_S(S,S)}{1+e^{-(S-\alpha_4)/\phi_4}} & \frac{SP_R(R,R)}{1+e^{-(R-\alpha_3)/\phi_3}} & \end{bmatrix}$$

Stress-free equilibria: $(x, N, S, R) = (0, 0, 0, A)$, $\left(\frac{K(r-m)}{r}, 0, 0, A\right)$, $\left(K, \frac{-m(1+e^{\lambda^*K-\mu})}{q\rho}, 0, A + \frac{-m(1+e^{\lambda^*K-\mu})}{q\rho}\right)$ where $A = N + R + S$ is the total human population. Notice the equilibrium $\left(K, \frac{-m(1+e^{\lambda^*K-\mu})}{q\rho}, 0, A + \frac{-m(1+e^{\lambda^*K-\mu})}{q\rho}\right)$ is not possible since $N < 0$

Jacobian at $(0, 0, 0, A)$:

$$J(0, 0, 0, A) - I\lambda = \begin{bmatrix} -r - m - \lambda & 0 & 0 & 0 \\ 0 & -r_1 - \lambda & 0 & 0 \\ 0 & r_1 & -r_2 - \sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2 - \sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues:

$$\lambda_1 = r - m, \lambda_2 = -r - 1, \lambda_3 = -r_2 - \sum_{z=1}^A \psi P_R, \lambda_4 = 0$$

Since we have a zero eigenvalue, the equilibrium is **unstable**.

Jacobian at $\left(\frac{K(r-m)}{r}, 0, 0, A\right)$:

$$J\left(\frac{K(r-m)}{r}, 0, 0, A\right) - I\lambda = \begin{bmatrix} m-r-\lambda & \frac{-qK(r-m)}{r(1+e^{\lambda^*K(r-m)/r-\mu})} & \frac{q\rho K(r-m)}{r(1+e^{\lambda^*K(r-m)/r-\mu})} & 0 \\ 0 & -r_1+r_1(r-m)-\lambda & r_3(r-m) & 0 \\ 0 & r_1-r_1(r-m) & -r_2+r_2(r-m)-r_3(r-m)-\sum_{z=1}^A \psi P_R - \lambda & 0 \\ 0 & 0 & r_2-r_2(r-m)+\sum_{z=1}^A \psi P_R & -\lambda \end{bmatrix}$$

Eigenvalues: After finding the determinant and setting equal to zero, we get

$$\begin{aligned} & \lambda \left[\lambda^3 + \left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right) \lambda^2 \right. \\ & + \left(mr_1 \sum_{z=1}^A \psi P_R - m \sum_{z=1}^A \psi P_R + r \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R - m^2 r_1 \right. \\ & - m^2 r_2 + m^2 r_1 r_2 + m^2 r_3 + mr_1 + 2mrr_1 - mr_2 + 2mrr_2 - 2mr_1 r_2 - 2mrr_3 + 2mr_1 r_3 \\ & \quad \left. - r^2 r_1 - r^2 r_2 + r^2 r_1 r_2 + r^2 r_3 - rr_1 + rr_2 - r_1 r_2 - 2rr_1 r_3 \right) \lambda \\ & + \left(mr_1 \sum_{z=1}^A \psi P_R - m^2 r_1 \sum_{z=1}^A \psi P_R + 2mrr_1 \sum_{z=1}^A \psi P_R - r^2 r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R \right. \\ & - m^3 r_1 r_2 + 3m^2 rr_1 r_2 - 2m^2 r_1 r_3 - 3mr^2 r_1 r_2 + mr_1 r_2 + 4mrr_1 r_3 + r^3 r_1 r_2 - 2r^2 r_1 r_3 \\ & \quad \left. \left. - rr_1 r_2 \right) \right] = 0 \end{aligned}$$

Using The cubic formula for finding the roots of a cubic polynomial, able to arrive at the following nonzero eigenvalues (Note we have one $\lambda = 0$ eigenvalue):

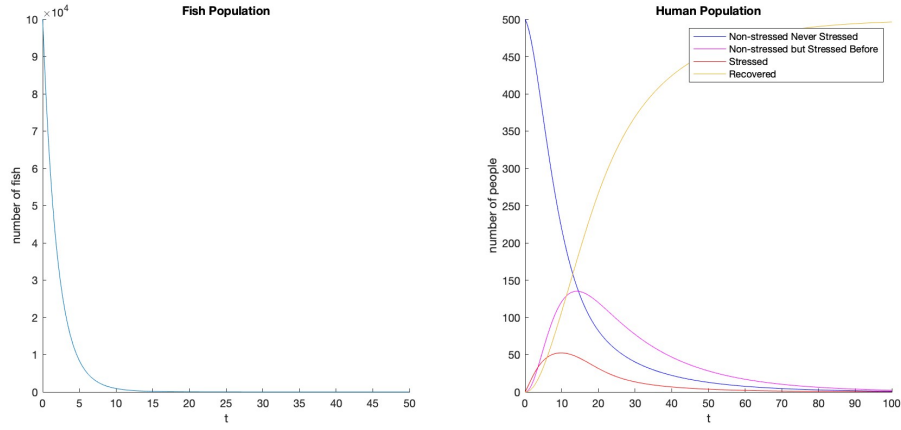
$$\begin{aligned}
\Delta_0 &= b^2 - 3ac \\
&= \left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right)^2 \\
&\quad - 3 \left(mr_1 \sum_{z=1}^A \psi P_R - m \sum_{z=1}^A \psi P_R + r \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R \right. \\
&\quad - m^2 r_1 - m^2 r_2 + m^2 r_1 r_2 + m^2 r_3 + mr_1 + 2mrr_1 - mr_2 + 2mrr_2 - 2mr_1 r_2 \\
&\quad \left. - 2mrr_3 + 2mr_1 r_3 - r^2 r_1 - r^2 r_2 + r^2 r_1 r_2 + r^2 r_3 - rr_1 + rr_2 - r_1 r_2 - 2rr_1 r_3 \right)
\end{aligned}$$

$$\begin{aligned}
\Delta_1 &= 2b^3 - 9abc + 27a^2d \\
&= 2 \left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right)^3 \\
&\quad - 9 \left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right) \\
&\quad \left(mr_1 \sum_{z=1}^A \psi P_R - m \sum_{z=1}^A \psi P_R + r \sum_{z=1}^A \psi P_R - r_1 \sum_{z=1}^A \psi P_R - rr_1 \sum_{z=1}^A \psi P_R \right. \\
&\quad - m^2 r_1 - m^2 r_2 + m^2 r_1 r_2 + m^2 r_3 + mr_1 + 2mrr_1 - mr_2 + 2mrr_2 - 2mr_1 r_2 \\
&\quad \left. - 2mrr_3 + 2mr_1 r_3 - r^2 r_1 - r^2 r_2 + r^2 r_1 r_2 + r^2 r_3 - rr_1 + rr_2 - r_1 r_2 - 2rr_1 r_3 \right) \\
&\quad + 27 \left(mr_1 \sum_{z=1}^A \psi P_R - m^2 r_1 \sum_{z=1}^A \psi P_R + 2mrr_1 \sum_{z=1}^A \psi P_R - r^2 r_1 \sum_{z=1}^A \psi P_R \right. \\
&\quad - rr_1 \sum_{z=1}^A \psi P_R - m^3 r_1 r_2 + 3m^2 rr_1 r_2 - 2m^2 r_1 r_3 - 3mr^2 r_1 r_2 + mr_1 r_2 \\
&\quad \left. + 4mrr_1 r_3 + r^3 r_1 r_2 - 2r^2 r_1 r_3 - rr_1 r_2 \right)
\end{aligned}$$

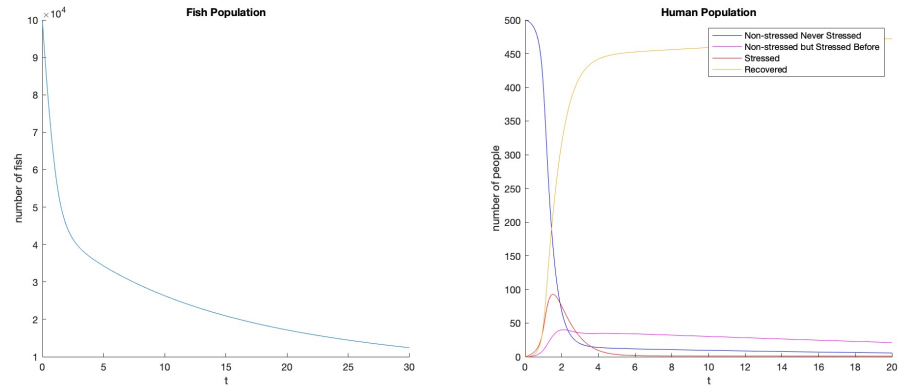
$$C_2 = \sqrt[3]{\frac{\Delta_1 \pm \sqrt{\Delta_1^2 - 4\Delta_0^3}}{2}}$$

$$\begin{aligned}
\lambda_i &= -\frac{1}{3a} \left[b + \xi^i C_2 + \frac{\Delta_0}{\xi^i C_2} \right] \text{ where } \xi = \frac{-1 + \sqrt{-3}}{2} \\
\lambda_0 &= -\frac{1}{3} \left[\left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right) \right. \\
&\quad \left. + C_2 + \frac{\Delta_0}{C_2} \right] \\
\lambda_1 &= -\frac{1}{3} \left[\left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right) \right. \\
&\quad \left. + \frac{-1 + \sqrt{-3}}{2} C_2 + \frac{\Delta_0}{\frac{-1 + \sqrt{-3}}{2} C_2} \right] \\
\lambda_2 &= -\frac{1}{3} \left[\left(\sum_{z=1}^A \psi P_R - m + mr_1 + mr_2 - mr_3 + r - rr_1 - r_1 - rr_2 + r_2 + rr_3 \right) \right. \\
&\quad \left. + \frac{-1 - \sqrt{-3}}{2} C_2 + \frac{\Delta_0}{\frac{-1 - \sqrt{-3}}{2} C_2} \right]
\end{aligned}$$

Since we know we have at least one zero eigenvalue, the equilibrium is **unstable**.

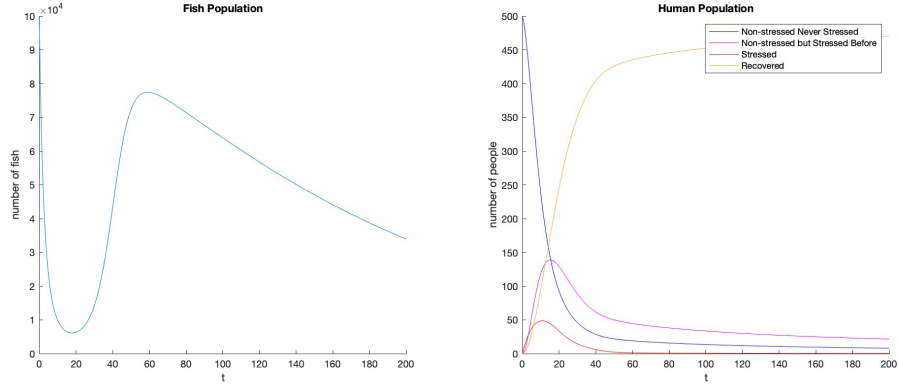


(a) This is a repeat of figure 1.3a with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5 years, the duration of the event is 74 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 52 . In addition, the amount of people that were able to skip the stressed state is ~ 106 .

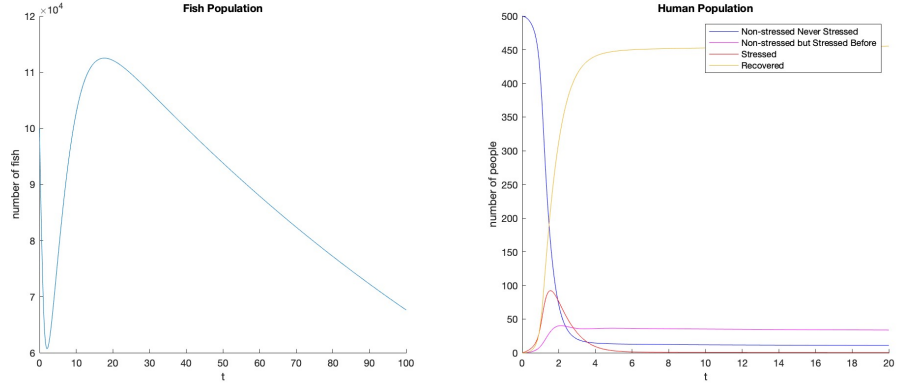


(b) Uses the same parameters as 1.8a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 20 years, the total number of people that become stressed is ~ 267 , and the peak number of stressed people is ~ 93 . The amount of people that skipped the stressed state is ~ 233 .

Figure 1.8: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.1 and 1.4.

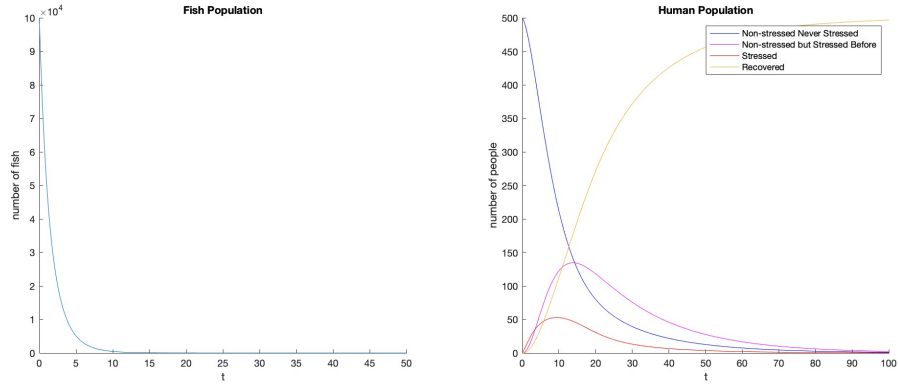


(a) This is a repeat of figure 1.3b with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5 years, the duration of the event is 65 years, the total number of people that become stressed is ~ 396 , and the peak number of stressed people is ~ 49 . In addition, the amount of people that were able to skip the stressed state is ~ 104 .

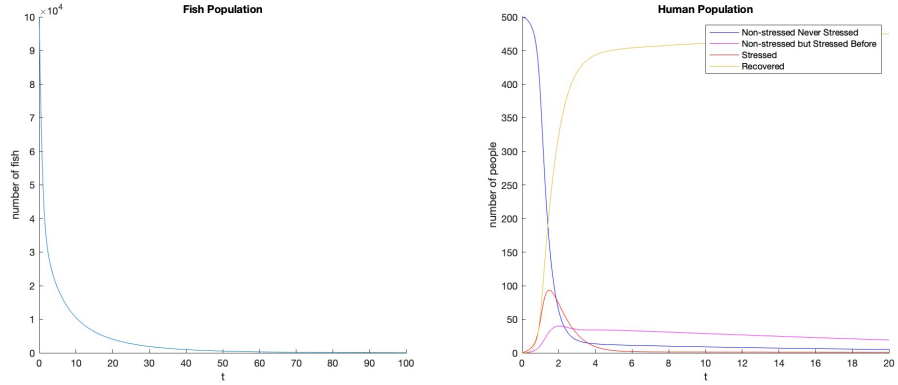


(b) Uses the same parameters as 1.9a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 6 years, the total number of people that become stressed is ~ 266 , and the peak number of stressed people is ~ 92 . The amount of people that skipped the stressed state is ~ 234 .

Figure 1.9: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.2 and 1.4.

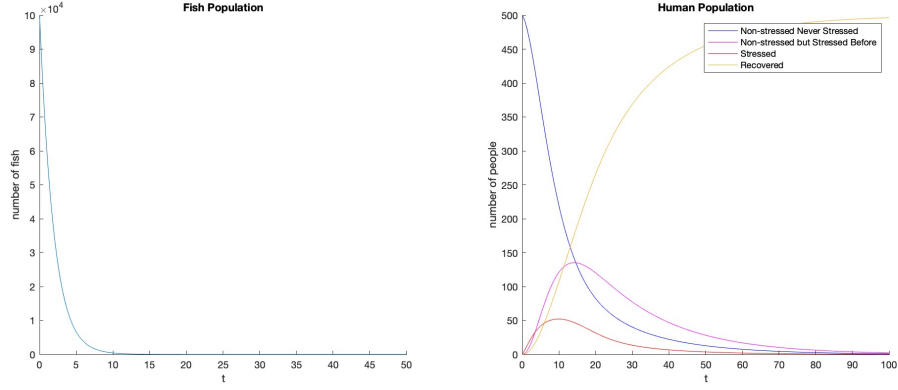


(a) This is a repeat of figure 1.3c with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 53 . In addition, the amount of people that were able to skip the stressed state is ~ 106 .

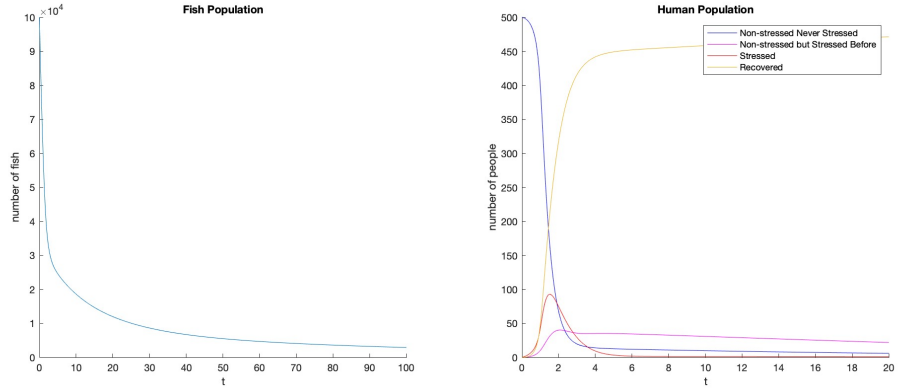


(b) Uses the same parameters as 1.10a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 20 years, the total number of people that become stressed is ~ 268 , and the peak number of stressed people is ~ 93 . The amount of people that skipped the stressed state is ~ 232 .

Figure 1.10: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.3 and 1.4.

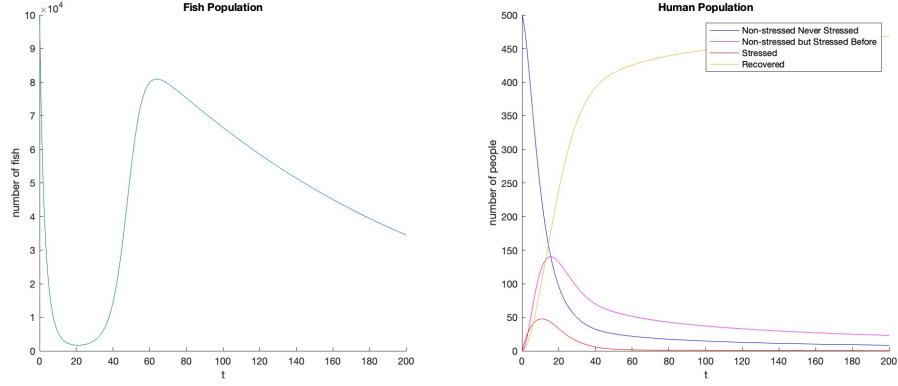


(a) This is a repeat of figure 1.4a with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 393 , and the peak number of stressed people is ~ 53 . In addition, the number of people who were able to skip the stressed state is ~ 107 .

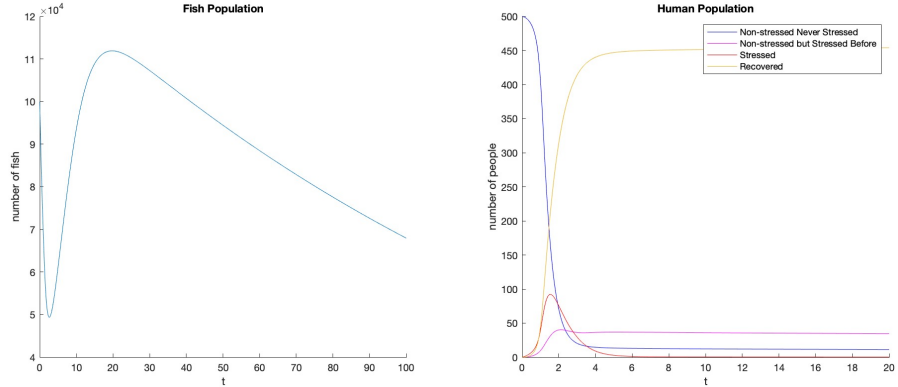


(b) Uses the same parameters as 1.11a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 20 years, the total number of people that become stressed is ~ 267 , and the peak number of stressed people is ~ 93 . The amount of people that skipped the stressed state is ~ 233 .

Figure 1.11: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.1 and 1.5.

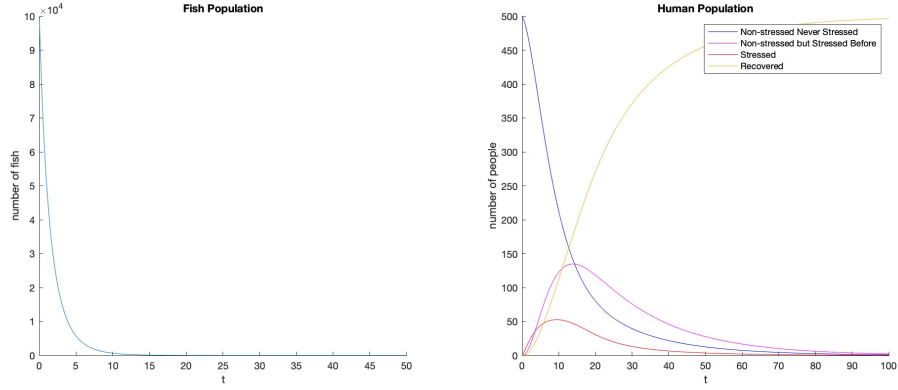


(a) This is a repeat of figure 1.4b with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5, the duration of the event is 58 years, the total number of people that become stressed is ~ 396 , and the peak number of stressed people is ~ 50 . In addition, the amount of people that were able to skip the stressed state is ~ 104 .

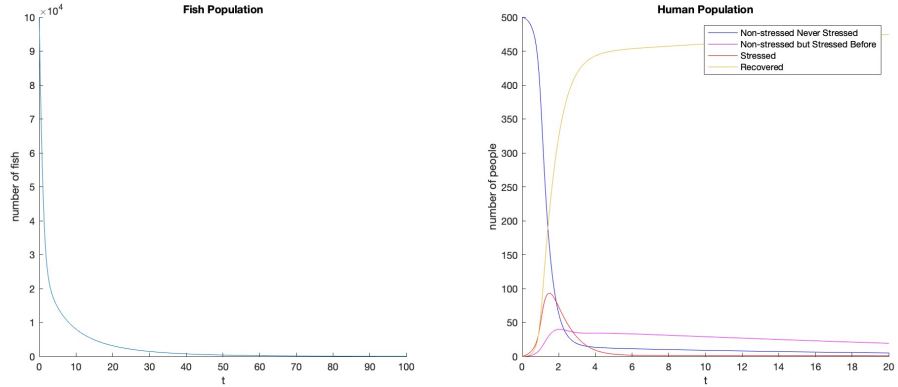


(b) Uses the same parameters as 1.12a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 7 years, the total number of people that become stressed is ~ 268 , and the peak number of stressed people is ~ 93 . The amount of people that skipped the stressed state is ~ 232 .

Figure 1.12: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.2 and 1.5.



(a) This is a repeat of figure 1.4c with a connectivity of $c = 0.01$. Again, the average time a person stressed is about 1.5 years, the duration of the event is 73 years, the total number of people that become stressed is ~ 394 , and the peak number of stressed people is ~ 53 . In addition, the amount of people that were able to skip the stressed state is ~ 106 .



(b) Uses the same parameters as 1.13a except for a change in connectivity to $c = 0.1$. The average time a person stressed is about 1 year, the duration of the event is 20 years, the total number of people that become stressed is ~ 267 , and the peak number of stressed people is ~ 93 . The amount of people that skipped the stressed state is ~ 233 .

Figure 1.13: Compares how a connectivity value of 0.01 compares with a connectivity value of 0.1 with the case combination of equations 1.3 and 1.5.

Chapter 2

Budget Allocation and Illegal Fishing: a Game Theoretic Approach

2.1 Abstract

Conservation efforts are under constant threat of failure due to poaching. Effort to combat poaching may take a number of forms, but access to each form depends on resources, and access to these resources may itself depend on the success of previous efforts (e.g., monetary donations from supporters could directly combat poaching, but may be more effective if partially spent on recruiting additional supporters who then also donate). We adopt a mathematical framework with inspiration from the famous ‘Colonel Blotto Game’ to model the ongoing battle between Conservationists and Poachers. Focusing on a marine setting as a case study, players have budgets consisting of three different types of resources: monetary, non-monetary, and supporters. The heterogeneous battlefields (laws, marine reserves, and community) reflect commonly employed conservation tactics meant to limit poaching. Conservationists allocate resources to limit the success of Poachers, while Poachers allocate resources to overcome barriers implemented by Conservationists. We assume that no action can succeed without supporters, and thus whichever player wins over all the supporters in the community (i.e., the community battlefield), wins the game. We analyze battlefield payoffs and player budget distributions to determine overall player success. We demonstrate how initially disadvantaged players may still have an opportunity to win the game, although we find success in the first few round can be most critical under certain scenarios. By framing the question in this way, we hope to provide additional tools for decision support to guide resource allocation, improving the efficacy of conservation efforts.

2.2 Introduction

Poaching is an ongoing issue threatening endangered species both across land and water habitats. Previous studies stress the critical status of endangered animals and their bleak future if poaching continues [69, 38, 46]. Low leopard populations in

Maputaland are a result of habitat loss, low food levels, and other factors including poaching [96]. Additionally overharvesting and poaching is contributing to the depletion of freshwater megafauna such as sturgeons, paddlefish, and the Cuban Crocodile [49]. Mathematical models provide insight for potential trajectories under current dynamics, different management strategies, or environmental change. The literature presents several models predicting future population levels. Some modeling techniques include statistical models [64], demographic models [110], and behavioral models [56], and have been used to give insightful information that helps target conservation efforts [87]. [30] uses Leslie matrices and Monte Carlo simulations to examine uncertainty in population growth rate. Models can also provide comparisons for different management strategies or intensities, further providing insight for implementation [48, 34]. Work presented by [5] creates a model and performs sensitivity analysis to conclude “protection of diverse coral communities with the presence, but not necessarily higher abundance, of thermally tolerant coral species and symbiont types, mitigation of additional anthropogenic impacts that affect coral–macroalgal competition, early coral life history stages, and coral survivorship, and protection of, and connectivity to, locations with oceanographic features that lead to lower thermal stress.”

Endangered species are often hunted for cultural or religious reasons. Shark finning is illegal in many countries, but a large black market encourages poaching. The majority of fin imports go to Hong Kong and other areas of China, where they are used in culturally significant shark fin soup [32]. Dating back to the Ming dynasty, shark fin soup has been served as a status symbol. It initially served as a tribute to the emperor due to the risk involved in catching the shark, but later animals known as being strong or fierce were additionally thought to strengthen whoever consumed them [26]. The cultural value of the fins create a market for poaching by having the potential to result in a large profit. Rhino horns also have an illegal market due to cultural demand. Vietnamese people value the horns for believed medical properties surrounding detoxifying [114].

Several methods are implemented to reduce poaching. Laws or restrictions for hunting and trading are often put in place to penalize partakers and discourage participation. However, due to high demand and high prices, poaching still occurs. The US enacted the 2000 Shark Finning Prohibition Act, the 2009 Shark Conservation Act, and the Shark Fin Trade Elimination Act in 2017 to reduce finning by prohibiting discarding finned bodies, requiring sharks to be landed with fins intact, and prohibiting the sale and possession of fins [41]. However, the US accounts for only a small percentage of the trade and it is argued that a ban on shark fins would compromise the US's influence on other countries' likelihood to adopt conservation models [103].

Community outreach and education programs can help in a variety of ways. One being the allowance of community members to participate in research or volunteer work, which allows the local community to become invested in the conservation effort [14, 75]. Additionally, creating advertisements such as billboards, media coverage, and short videos can help inform the public the critical condition of the species as well as the possible danger of consumption [39]. Often local communities are not aware of the damage their actions are doing, making the education of adults and children critical [71]. Marine reserves restrict human interaction and are used to protect species by giving them a haven of recovery. They can put quotas on fishing, limit the number of vessels, limit fishing time, as well as many other restrictions [71]. All of these management strategies can be used simultaneously to give endangered species a chance at recovery.

Game theory is a mathematical technique that is used to study player interactions and predict outcomes that depend of the decisions of other player(s). Famously, game theory is used in finance, economics, military, politics, as well as other fields. One famous game is the Prisoners Dilemma in which players can choose to betray the others. Their choice to betray or be loyal to the other prisoner affects the outcome for them both [16]. Another famous game, and the one that serves as a basis for the methods in this paper, is the Colonel Blotto game in which two players allocate

resources to different battlefields in the hopes of either winning the most battlefields or the most payoff. Battlefields can represent different platforms depending on the scenario in which the game is applied. The Colonel Blotto game has been used to explain social scenarios [63], network systems [45], and military strategy [28]. For military scenarios, battlefields can be land regions while for network systems, battlefields can be transmissions when looking at radio jamming attacks [119].

This paper uses the Colonel Blotto game to address the issue of poaching where the players are Conservationists and Poachers. Players compete against each other by allocating a set number of resources to different areas or battlefields that contribute to the Poachers’ success at undermining conservation efforts and harvesting the species or the Conservationists’ success at restricting poaching. Extensions have been made to the basic format of the game to allow asymmetrical budgets [51]. Heterogeneous battlefields in which one battlefield is worth more than others is also considered. [102] proposes a solution to the case of both asymmetrical budgets and heterogeneous battlefields under certain conditions. We will adopt this framework in our model with the addition of sub-battlefields and player budgets consisting of three different resource types: monetary resources, non-monetary resources, and supporters. Monetary resources are money or economic resources, non-monetary resources are items such as boats, nets, and other physical equipment, and supporters are members of the community that either provide conservation support or a market for Poachers to sell to. Players distribute each of their resource types by choosing from nine different strategies to three different battlefields: laws, marine reserves, and community. Each battlefield contributes to the overall payoff of the game in varying amounts, depending on the influence it has on the success of the players. To account for the different resource types in the budget, sub-battlefields corresponding to the resource types were built into each battlefield category with the weight of each sub-battlefield depending on the influence of each resource type on the battlefield. Additionally, institutional memory can be set to either “no memory”, “memory of last round”, or “memory of all previous rounds”, which determines the information

the players have when making a current strategy decision. The strategies players choose from was designed by deciding on actions players may reasonably take in order to face their opponent.

It is worth mentioning that another resource allocation game is multi-armed bandit (MAB) problems in which a single player must allocate resources to different projects to either receive initially high rewards or to potentially have a higher delayed reward [72]. However, these problems only consists of one player and not two players competing, differing from the game presented here.

In this paper, we approach the issue of poaching by using the Colonel Blotto Game framework in a novel approach by introducing a budget involving different resource types along with battlefields that correspond to impactful areas of conservation. Additionally, we add sub-battlefields within each battlefield to correspond to the different resource types and the influence each resource has on that specific battlefield. We consider how the community support of either conservation or the continuation of poaching affects the success of each player.

2.3 Methods

The game theory model presented in this paper follows the framework of the famous Blotto game and explores how different strategies can affect the outcome of Conservationists fighting against illegal fishing [97, 9]. Both Conservationists and Poachers have budgets consisting of resources that they allocate to different battlefields in the hopes of gaining an advantage over their opponent. The budget resources consist of monetary resources, non-monetary resources, and supporters while the battlefields are laws, marine reserves, and the community. The game consists of several rounds, with the budget for the proceeding round reflecting the outcome of the previous. A round refers to players allocating resources and the determination of who won each sub-battlefield based on who allocated more resources to that sub-battlefield. Although evolutionary game theory depends on previous game

results, it combines population ecology and game theory and makes use of replicator equations for the evolution of strategies or traits [105, 106]. Here, we have the same player budgets dependent on previous round payoffs, which differs from traditional evolutionary game theory approach.

Supporters or the support of the community is the driver of the game. Supporters for Conservationists are community members that provide aid for conservation efforts by giving money or spread positive attitudes for conservation. Supporters for Poachers are community members that provide a market for Poachers to sell to and encouraging the continuation of poaching because of its cultural or social value. A player has the community's support when their supporter budget category consists of the majority of the community. The winner of the game is the player who wins the entire community's support. Once a player has the community's support, the other player either loses funding for conservation efforts or a market to sell into, making their efforts fruitless. Players can increase their number of supporters by allocating their resources effectively.

There are a few assumptions to the model that must be considered. Firstly, the budgets of each player are only known to themselves, and therefore they do not know the budgets of their opponent. Secondly, the community is a fixed value, meaning that there is no flux of incoming or departing people. Resources such as boats, fishing gear, etc. are fixed across rounds, meaning that neither player is significantly investing in the creation of new equipment. Their goal is to use their equipment efficiently. And lastly, every player must start a game with nonzero values for each budget category.

Our model provides insight to how a budget can be allocated to give the best chance of winning the game.

2.3.1 Player Budgets

Conservationists and Poachers have a variety of different resources that collectively contribute to their goal. As described earlier, resources can be described as monetary,

non-monetary, and supporters. We reflect the different resource categories through designing player budgets to reflect the three categories. The players' budgets are expressed as three-dimensional vectors $(\vec{C}, \vec{P})$ containing values for monetary, non-monetary, and supporters resources. The non-monetary category, containing resources such as ships, fishing gear, and equipment is a fixed value across rounds since it is assumed neither player is creating or destroying a significant amount of equipment. The supporters category is the proportion of the community that supports the efforts of the prospective player. Since every member of the community has to be accounted for, if Conservationists have the support of 40% of the community, Poachers have the remaining 60%. The monetary resources are dependent on how many supporters the player has. For Conservationists, monetary resources come from supporter donations, tax collection, or other money collection methods. For Poachers, monetary resources come from the market supporting the harvest of the illegal species. If the Poachers do not have a market to sell to, they lose all their funding to continue with the illegal activity.

Equations 2.1 and 2.2, show how the budgets of each player is calculated. The components of the vectors are [monetary, non-monetary, supporters]. An example scenario is described in the following parameters. $c_1 = .4$, meaning Conservationists have 40% of the community population as supporters. $a_1 = 8$, meaning each supporter contributes an average of \$8.00. Meanwhile, the Poachers have the remaining 60% of the population, making $c_2 = 1 - c_1 = 0.6$. Each Poacher supporter contributes an average of \$5.00, making $a_2 = 5$. $b_1 = 200$ and $b_2 = 150$, which are the non-monetary resources of Conservationists and Poachers respectively.

$$\vec{C} = [a_1(c_1(\text{population})), b_1, c_1(\text{population})] \quad (2.1)$$

$$\vec{P} = [a_2(c_2(\text{population})), b_2, c_2(\text{population})] \quad (2.2)$$

After each round is won, the budgets are reevaluated based off of the payoff of the previous round, with the redistribution of the community being the driving factor.

2.3.2 Battlefield Operation and Payoff

Although there are many different areas where Conservationists could make an impact, and different areas Poachers must navigate in order to continue their practice, we have chosen to focus on three main categories: laws, marine reserves, and community. Therefore, we designed three battlefields corresponding to laws, marine reserves, and community. Laws encompass policy creation and enforcement for the Conservationists and encompasses policy repeal and ramification avoidance for Poachers. Marine Reserves include the creation and patrolling of areas deemed a marine reserve for Conservationists, while for Poachers, it includes police avoidance and the ability to operate effectively in the protected area. The community battlefield involves winning over supporters through campaigning, education, emphasis on traditions, or other outreach techniques. A payoff bank is set at the beginning of the game assigning each battlefield a percentage according to the contribution it has on the system. Ultimately, the player with the highest payoff wins the round. Equation 2.3 gives a vector representing a payoff distribution. The components correspond to laws, reserves, and community respectively. So, for example, if $p_1 = 0.15$, $p_2 = 0.3$, and $p_3 = 0.55$, then laws have a payoff of 15% of the payoff bank, reserves have 30% of the payoff bank, and community 55% of the payoff bank. It is a requirement that all the probabilities sum to one so the entirety of the payoff bank is accounted for without allotting more than exists.

$$\text{Payoff Distribution} = [p_1, p_2, p_3] \quad (2.3)$$

Within each battlefield, there are three sub-battlefields corresponding to the players' monetary, non-monetary, and supporter resources. This is to ensure budget categories are compared in comparable terms since, for example, is it not known how one non-monetary resource compares to one supporter. Additionally, one resource type may affect one battlefield category more than the other resource types. To account for this, each sub-battlefield contains a proportion of the battlefield's payoff

corresponding to how much effect it would have its parent battlefield. This creates a payoff matrix found in expression 2.4. The columns are the laws, reserves, and community battlefields while the rows are the monetary, non-monetary, and supporters sub-battlefields. Equation 2.5 gives the payoff matrix parameter values used for analysis. It assigns 55% of the laws battlefields to the monetary sub-battlefield, 20% to the non-monetary sub-battlefield, and 25% to the supporters sub-battlefield. Similar assignments are made for reserves and community battlefields. The monetary sub-battlefield holds the most for laws, non-monetary for the marine reserves sub-battlefield, and supporters for the community sub-battlefield. These could be altered to be scenario specific, however we believe this gives a useful representation. It is required that the percentages on the sub-battlefields with its parent battlefield sum to one. Unlike player budgets, battlefield payoffs do not depend on previous rounds. The payoff matrix set at the beginning of the game remains fixed through the duration of the game.

$$\begin{array}{c}
 \text{laws payoff} \quad \text{reserves payoff} \quad \text{community payoff} \\
 \begin{array}{c} \text{monetary} \\ \text{non-monetary} \\ \text{supporters} \end{array} \left(\begin{array}{ccc} lm & rm & cm \\ ln & rn & cn \\ ls & rs & cs \end{array} \right) \quad (2.4)
 \end{array}$$

$$\begin{array}{c}
 \text{laws payoff} \quad \text{reserves payoff} \quad \text{community payoff} \\
 \begin{array}{c} \text{monetary} \\ \text{non-monetary} \\ \text{supporters} \end{array} \left(\begin{array}{ccc} 0.55 & 0.3 & 0.3 \\ 0.2 & 0.5 & 0.1 \\ 0.25 & 0.2 & 0.6 \end{array} \right) \quad (2.5)
 \end{array}$$

The implementation of the payoff matrix allows for the battlefield to distribute its payoff to both players according to the resources they allocated to it.

2.3.3 Strategies

Both players have the ability to choose from nine different strategies. They are listed below with supplementary examples as needed. Although the different strategies players can implement may exceed the ones listed here, we have chosen the following strategies by evaluating logical choices the player may make. We do not consider all possible options since some allocations do not provide a viable strategy for reasonable players to make. Depending on the application of this model, some strategies can be removed or different strategies may be added. The players know the payoff distribution and may make decisions reflecting battlefield and sub-battlefield influences or payoff weights. Players may choose to allocate the majority of their resources to the battlefield or sub-battlefields containing the potential for the most payoff. Additionally, since the community battlefield ends the game once a player wins the community's support, players may choose to allocate more resources to the community battlefield. However, players may also attempt to predict what their opposition might do and allocate resources to battlefields they think their opposition might neglect. For example, they may anticipate their opposition allocating most resources to the highest paying battlefield or sub-battlefield and, therefore, allocate most of their resources to one or both the other battlefields or sub-battlefields.

1. **Even:** Allocate resources evenly across all battlefields and sub-battlefields
2. **Dominant Sub-Battlefield:** Allocate all resources of a particular type to the sub-battlefield that contributes the most payoff for that battlefield. If the same sub-battlefield type contributes the most in two different battlefields, then the resources are split according to how much more one battlefield contributes than the other. If all three battlefields have the same top contributing sub-battlefields, distribute resources evenly across battlefields

- Ex: If the sub-battlefield in the battlefield laws that contains the most payoff contribution is monetary (0.55) and if the sub-battlefield in the reserves battlefield that has the most payoff contribution is monetary (0.5) then $\frac{.55}{.5} = 1.1$ more resources would go towards the laws battlefield. So if the budget is 100, $1.1x + x = 100 \implies x = 100/2.2 = 47.619$ would go towards the laws battlefield and 52.381 would go to reserves battlefield. The category not accounted for is distributed across battlefields according to the contribution of the battlefields

3. **Proportional Non-dominant Sub-battlefields:** Allocate resources of a particular type to the sub-battlefields that do not contribute the highest payoff. That way, they can win the most payoff from that battlefield without winning the highest paying sub-battlefield. If two battlefields share the same sub-battlefield as the second(third) most contributing, then split the resources proportionally to how much they contribute similar to the example in Strategy 2. If all three share the same second(third) contributing sub-battlefield, distribute evenly across battlefields. If one battlefield shares a second highest contributing sub-battlefield with a third contributing sub-battlefield in a different sub-battlefield, then all the resources go to the battlefield that has the second highest contributing sub-battlefield
4. **Disproportional Non-dominant Sub-battlefields:** Allocate resources of a particular type to the sub-battlefields that do not contribute the most payoff, but if two battlefields share a second(third) sub-battlefield, then the majority (90-95%) goes to the battlefield that contributes the most while a minority (5-10%) go to the other.
5. **Dominant Battlefield:** If the payoff of the battlefield with the most payoff contribution is greater than the sum of the payoff contributions from the two remaining battlefields, then allocate all resources of all types to the battlefield that contributes the most.

If the payoff of the battlefield with the most contribution is less than the sum of the contributions from the two remaining battlefields, then split all resources proportionally (same as in the example of Strategy 2) of all types to the two battlefields that do not contribute the most payoff.

6. **Proportional Battlefields:** Distribute resources accordingly to how much payoff contribution the battlefield holds.
 - Ex: If the laws battlefield hold 15%, the reserves battlefield 30%, and the community battlefield 55%, then 15% of the monetary, non-Monetary, and supporter budgets would go to the laws battlefield, 30% of the monetary, non-monetary, and supporter budgets would go to the reserves battlefield, etc.
7. **Community:** Always allocate all resources to the community battlefield because the more supporters a player has, the larger their supporter and monetary budgets will be for the next round.
8. **Dominant Two Battlefields:** Allocate resources proportionally to the the top two battlefields with the highest payoff similarly to the method in the Strategy 2 example. If all battlefields have equal payoff, allocate resources evenly across battlefields
9. **Dominant and Community Battlefields:** Allocate resources proportionally to the battlefield with the highest payoff and the community battlefield similarly to the method in the Strategy 2 example. If all battlefields have equal payoff, allocate resources evenly across battlefields

2.3.4 Institutional Memory

Since humans have the ability to retain information which can influence their decisions, game theory approaches commonly involve memory attributes where players can remember a capacity of previous results and adapt their decision accordingly [79]. We have incorporated three different scenarios of institutional memory to analyze three different application instances introduced in the following descriptions. Institutional memory can be set at the beginning of the game to be either “no memory”, “memory of last round”, and “memory of all previous rounds”. Players are the Conservationist and Poacher groups, so while individual members make up the groups, the groups as a whole hold the institutional memory setting. Both players are required to have the same institutional memory.

If “no memory” is selected then, in every round, both players have equal probability of selecting any of the nine strategies. A scenario such as this represents a case where the turnover for either Poachers, Conservationists, or both correspond with the time frame of the rounds. This means that there is a new group of Poachers or Conservationists each round. Since there is no one left from the previous round to share which strategy was used, the current members only know the outcome, not the method, and therefore has to make a decision independent of the strategy chosen in the previous round.

If “memory of last round” is selected, then the results of the previous round influence the strategy decision. Similar to the “no memory” scenario, there could exist a turnover in at least one of the player categories. However, the turnover is longer than the time frame of a round and shorter than the time frame of two rounds. This means there exists people from the previous round to inform which strategy led them to the current results and current budgets. After one round, the information is lost as the people present during two rounds ago are replaced by new members. If the player won the previous round, then the player has a predetermined probability of adopting the previous strategy. Equation 2.6 illustrates how the probability of

adoption is calculated.

$$P(\text{adopting previous strategy}) = \frac{\text{payoff won in previous round}}{\text{Payoff Bank}} \quad (2.6)$$

If the previous strategy is not adopted then, then players have equal probability of choosing any of the nine strategy, as they would if they had “no memory”.

Lastly, if “memory of all previous rounds” is selected, then players remember the outcomes of all previous rounds, giving them the option of replaying the strategy that awarded them the highest payoff. A case of “memory of all previous rounds” represents a scenario where Poacher and Conservationist members maintained excellent records of previous strategies used and the corresponding results for current members to refer to when approaching a new round. The probability of adopting the most successful previous strategy is found by using equation 2.6. No matter which institutional memory scenario is chosen, the game is over when one player wins the support of the entirety of the community. The winner being the player with the highest payoff from the last round.

2.3.5 Playing the Game

A game is made up of one or more rounds in which each player chooses a strategy and allocates their budget. The outcome determines who won the round, or if one player has collected the entire community as supporters, who won the game. If the community is still split between players, the budgets for the next round are determined by the outcome of the previous round. The winner of the round is the player with the highest awarded payoff.

2.4 Results

In order to understand the outcome of the game and potentially aid in decision making, the results from a single round played with budgets adopting extreme cases

are compared. Extreme cases are where players have a budget containing a large amount of one resource and a minimal amount of the other two. The values selected as the large and small amounts are arbitrary and could have been chosen differently as long as they are sufficiently large or small respectively.

The different extreme player budget cases account for different applicable scenarios. For example, if Conservationists have high monetary resources and Poachers have high supporters, then this could represent a case where poaching has cultural or religious value, but a portion of taxes go toward methods to reducing illegal fishing. An example of this is the importance of sharks in Chinese and Hawaiian cultures. For the Chinese, it originated as a delicacy reserved for the emperor or the wealthy, while in Hawaii, sharks are rarely eaten, but hold religious significance such as being influential spirits [32].

If Conservationists have high supporters and Poachers have high monetary resources, then it could mean that Conservationists have a lot of supporters, but do not have effective fund raising methods or governmental aid. Community conserved areas (CCAs) are areas that are protected via community based rules and regulations and are most common among indigenous or rural communities [88]. Meanwhile, Poachers are selling the illegal species at an inflated price so not many customers are required. Whale Sharks are a highly conserved species of shark with consequences such as high fees and imprisonment for poaching or market participation, but areas such as Indonesia still have issues with poaching due to the high price of the fish [85].

We are assuming that if either player has high non-monetary resources, it is due to a previous acquirement of the resources. Non-monetary resources are fixed throughout the game meaning that a significant amount of equipment or other non-monetary resources is not gained or lost throughout the game.

Additional to single round results with extreme player budgets, heatmaps of full game outcomes give results of player wins according to how many rounds the game consisted of and the institutional memory setting. Together these analyses provide a basis for predicting player outcomes and strategy suggestions for desirable results.

2.4.1 Single Round Comparisons of Player Budget Extremes

In order to predict a player's outcome after one round of play, each player's possible strategies are played against all the other player's strategies and the payoff distribution is depicted by heatmaps. Figure 2.1 provide the distributions for each player in the extreme scenarios. That is, when a player has a large amount of one resource and minimal amount of the other two. Since all people in the community must be accounted for, if one player has the majority of the population as supporters, then the other player must have the minority. This reduces the number of combinations significantly. Figures 2.2-2.4 provide the same information as in figure 2.1 scaled to allow examination of each plot in greater individual detail rather than focusing on comparative outcomes. Further, box plots of single round comparisons can be found in the Appendix (figures 2.9 - 2.20). In addition to the consideration of budget extremes, different battlefield payoff distributions are considered, including even battlefield payoffs, the majority going to the community battlefield with the resources battlefield having twice the payoff as the laws battlefield, and the majority going to the community battlefield with the resources battlefield having half the payoff as the laws battlefield. The community battlefield carries the most contribution in the non-equal battlefield payoff scenarios due to the community being the driving factor for both the game termination and the next round monetary budget. The Payoff Bank value is 100 and the community population is 100 persons.

Assuming the players do not know the budgets of the other player but do know the battlefield payoff distribution, then we can analyze which strategies would give optimal results for each of the players. Figure 2.1(1) gives battlefield payoff vector as [Laws, Marine Reserves, Community]=[.15 .3 .55]. If Conservationists have high supporters, then they should either play the 'Even', 'Proportional Battlefields', 'Dominant Two Battlefields', or 'Dominant and Community Battlefields' strategy with 'Even' and 'Proportional Battlefields' having the potential for the highest payoff. Meanwhile if Poachers have high supporters, they should also play either

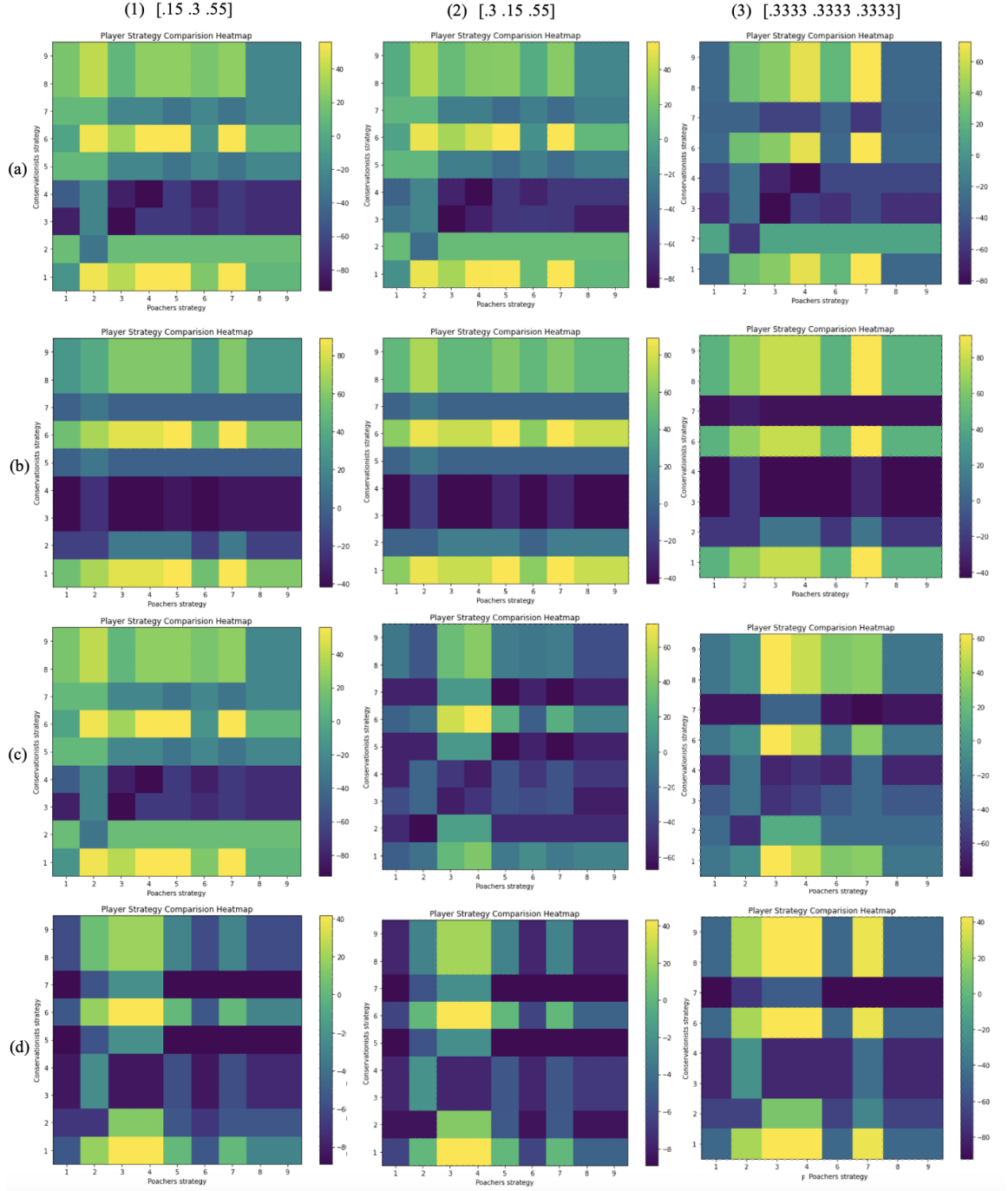
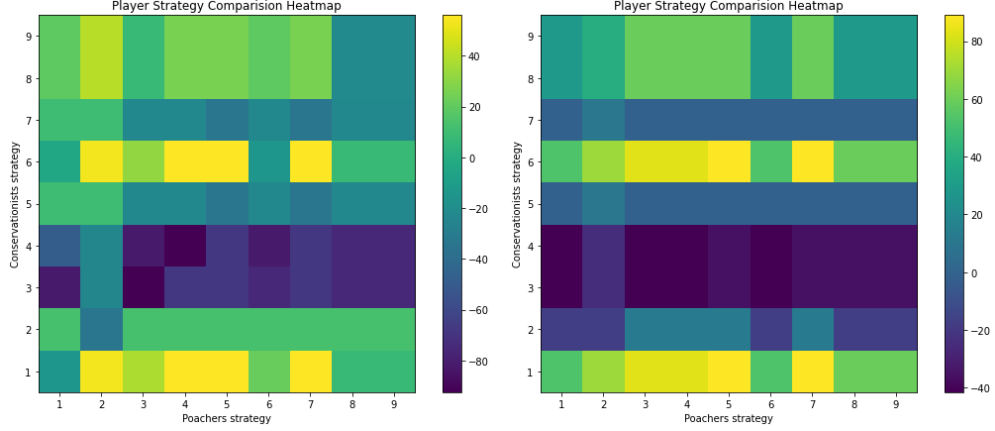
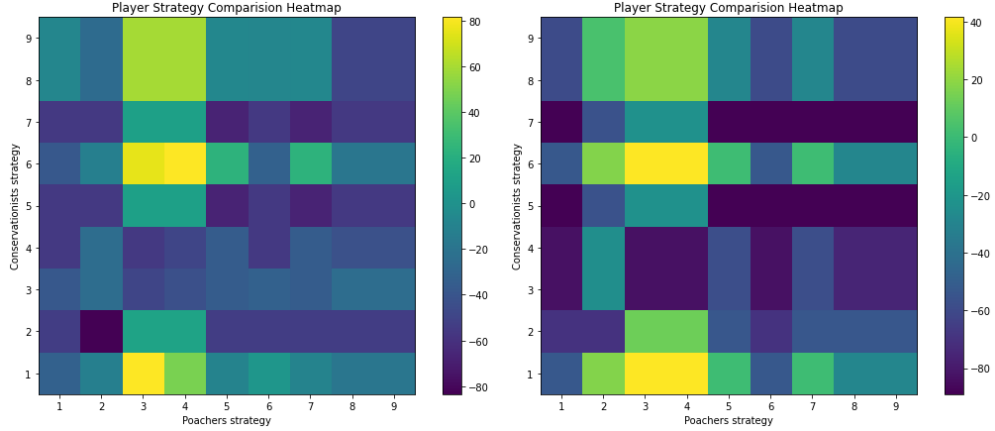


Figure 2.1: Column 1 represents when battlefield payoff distribution is (Laws, Marine Reserves, Community)=(.15 .3 .55). Column 2 represents when battlefield payoff distribution is (Laws, Marine Reserves, Community)=(.3 .15 .55). Column 3 represents when battlefield payoff distribution is even. That is, (Laws, Marine Reserves, Community)=(.3333 .3333 .3333). For row (a) and (b), the budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)) in (a) and (Low, High, Low)=(1*(People), 200, .1*(Population)) in (b). For row (c) and (d), the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Conservationists is (High, Low, Low)=(20*(People), 10, .1*(Population)) in (c) and (Low, High, Low)=(1*(People), 200, .1*(Population)) in (d).

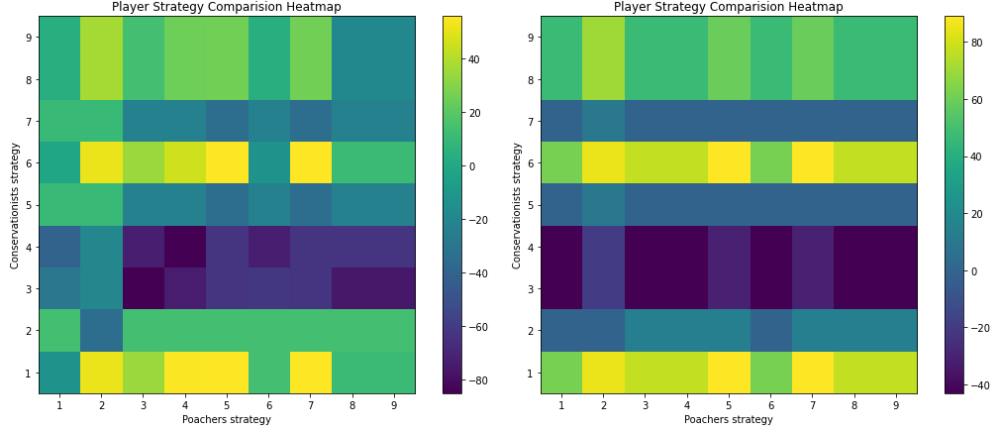


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1 and 6 give Conservationists the highest winning payoff difference while 1, 6, 8, and 9 give Poachers the highest chance of winning the round when they have high non-monetary resources. Strategies 6, 8, and 9 give Poachers the highest chance of winning when they have high monetary resources. Negative values represent Poachers winning while positive values represent Conservationists winning the round.

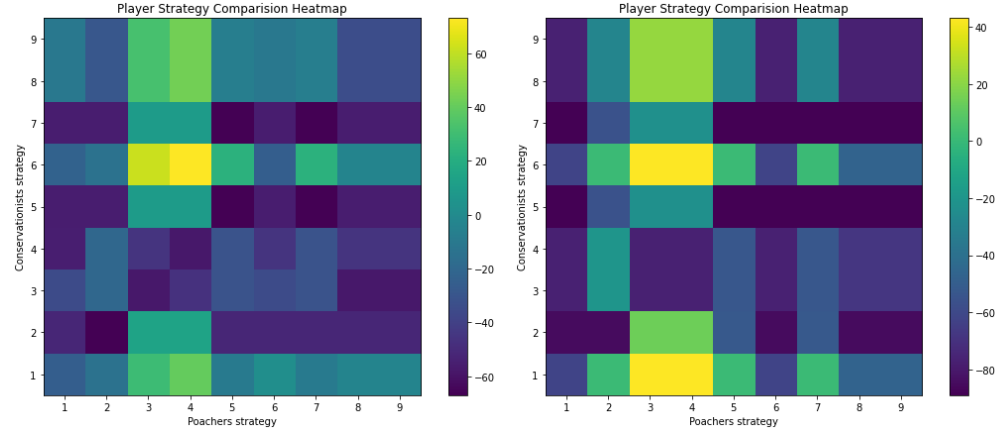


(b) The budget for Poachers is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Conservationists is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1, 6, 8, and 9 give Poachers the highest winning payoff difference when Conservationists have high non-monetary resources while 1 and 6 give Conservationists the highest chance of winning. When Conservationists have high monetary resources, strategies 8 and 9 give Poachers the highest chance of winning. No strategy will guarantee Conservationists will win. However, strategy 6 has the highest chance of giving Conservationists a winning payoff. Negative values represent Poachers winning while positive values represent Conservationists winning the round.

Figure 2.2: Battlefield payoff distribution is [Laws, Marine Reserves, Community]=[.15 .30 .55]

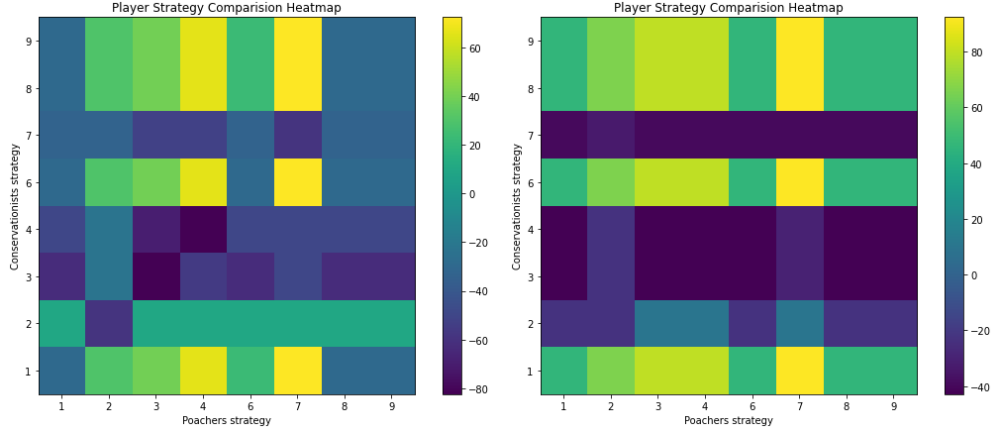


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1 and 6 give Conservationists the highest winning payoff difference when Poachers have high non-monetary resources while 1 and 6 give Poachers the highest chance of winning. When Poachers have high monetary resources, strategies 1 and 6 give Conservationists the highest chance of winning. No strategy will guarantee Poachers will win. However, strategy 8 and 9 has the highest chance of giving Poachers a winning payoff. Negative values represent Poachers winning while positive values represent Conservationists winning the round.

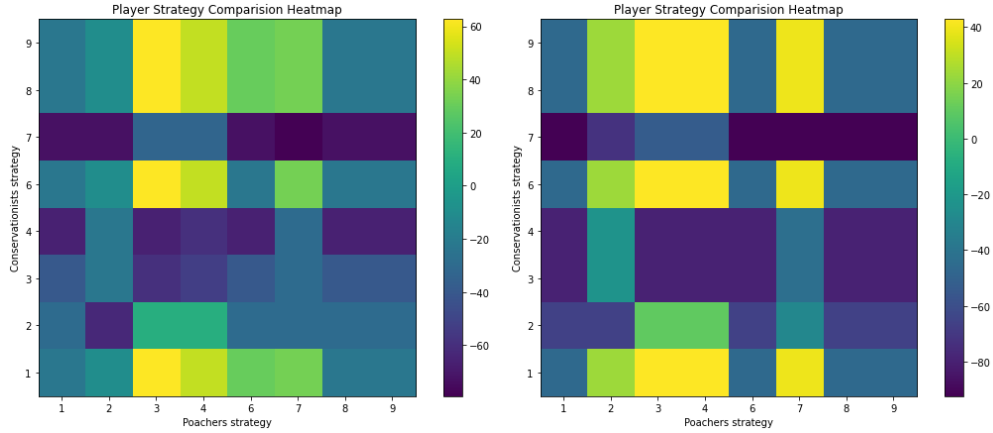


(b) The budget for Poachers is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Conservationists is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1, 6, 8, and 9 give Poachers the highest winning payoff difference when Conservationists have high non-monetary resources while 1 and 6 give Conservationists the highest chance of winning. When Conservationists have high monetary resources, strategies 8 and 9 give Poachers the highest chance of winning. No strategy will guarantee Conservationists will win. However, strategy 6 has the highest chance of giving Conservationists a winning payoff. Negative values represent Poachers winning while positive values represent Conservationists winning the round.

Figure 2.3: Payoff distribution is [Laws, Marine Reserves, Community]=[.30 .15 .55]



(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1, 6, 8, and 9 give Conservationists the highest winning payoff difference when Poachers have high non-monetary resources while 1, 6, 8, and 9 give Poachers the highest chance of winning although no strategy guarantees they will win. When Poachers have high monetary resources, strategies 1, 8, and 9 give Conservationists the highest chance of winning. Strategies 1, 8, and 9 has the highest chance of giving Poachers a winning payoff. Negative values represent Poachers winning while positive values represent Conservationists winning the round.



(b) The budget for Poachers is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Conservationists is (High,Low, Low)=(20*(People), 10, .1*(Population)) on the left and (Low, High, Low)=(1*(People), 200, .1*(Population)) on the right. Strategies 1, 6, 8, and 9 give Poachers the highest winning payoff difference when Conservationists have high non-monetary resources while 1, 6, 8, and 9 give Conservationists the highest chance of winning although no strategy will guarantee Conservationists will win. When Conservationists have high monetary resources, strategies 1, 8, and 9 give Poachers the highest chance of winning. No strategy will guarantee Conservationists will win. However, strategies 1, 8, and 9 has the highest chance of giving Conservationists a winning payoff. Negative values represent Poachers winning while positive values represent Conservationists winning the round.

Figure 2.4: Payoff distribution is even ([Laws, Marine Reserves, Community]=[.3333 .3333 .3333])

the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategy. If Conservationists have high monetary resources, Poachers have the advantage, but Conservationists should play the ‘Proportional Battlefields’ strategy to have the highest chance of winning the round. If Poachers have high monetary resources, they are at a disadvantage but should play ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategy to have the highest chance of winning the most payoff. If Conservationists have high non-monetary resources, then they should play either the ‘Even’ or ‘Proportional Battlefields’ strategy to have the potential for the highest payoff and the highest probability of winning the game. If Poachers have high non-monetary resources, they should play either the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategy to have the highest chance of winning the most payoff.

In the scenario that the battlefield payoff distribution is [Laws, Marine Reserves, Community]=[.3 .15 .55] (Figure 2.1(2)), then if Conservationists have high supporters, then they should either play the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategy to ensure winning the round while if Poachers have high supporters, then they should either choose the ‘Even’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields strategy’. If Conservationists have high monetary resources, then the ‘Proportional Battlefields’ strategy gives them the highest chance of winning, while if Poachers have high monetary resources, then the ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, and ‘Dominant and Community Battlefields’ strategies give the highest chance of winning the round. If Conservationists have high non-monetary resources, then the ‘Even’ and ‘Proportional Battlefields’ strategies give the highest chance of winning the round and the potential for the highest payoff. If Poachers have high non-monetary resources, then similarly, the ‘Even’ and ‘Proportional Battlefields’ strategies would give them the highest chance of winning the round.

Lastly, if the battlefield payoff is equally distributed ([Laws, Marine Reserves, Community]=[.3333 .3333 .3333]) (Figure 2.1(3)), then the ‘Dominant Battlefield’ strategy cannot be played due to constraints on that strategy. If Conservationists have high supporters, then the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategies gives the highest chance of winning the round along with the highest potential payoff. If Poachers have high supporters, then the ‘Even’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategies will almost guarantee Poachers win the round. Otherwise, the Poachers have a high chance of winning the round. For both players, if they have high monetary resources, then the ‘Even’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategies will give them the highest chance of winning the most payoff. Additionally, for both players, if they have high non-monetary resources, then the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategies give the highest chance of winning the round.

2.4.2 Comparisons of Memory and Round Quantity

In order to analyze how different institutional memory and the number of rounds affect the winner of the game, figure 2.5 show heatmaps of win frequency based on institutional memory and the number of rounds in the game. Figures 2.6-2.8 reproduce the heatmaps in 2.5 to show greater detail, while 2.5 provides easier comparison among the outcomes. Additionally, histograms of player win distribution and number of rounds can be found in the Appendix (figures 2.21 - 2.38). Each scenario runs 1,000 games and plots which player won the most rounds and indicate by how much. The negative values indicate Poachers winning more games than Conservationists while positive values indicate Conservationists winning more games than Poachers. Larger relative numbers show a larger difference in the number of

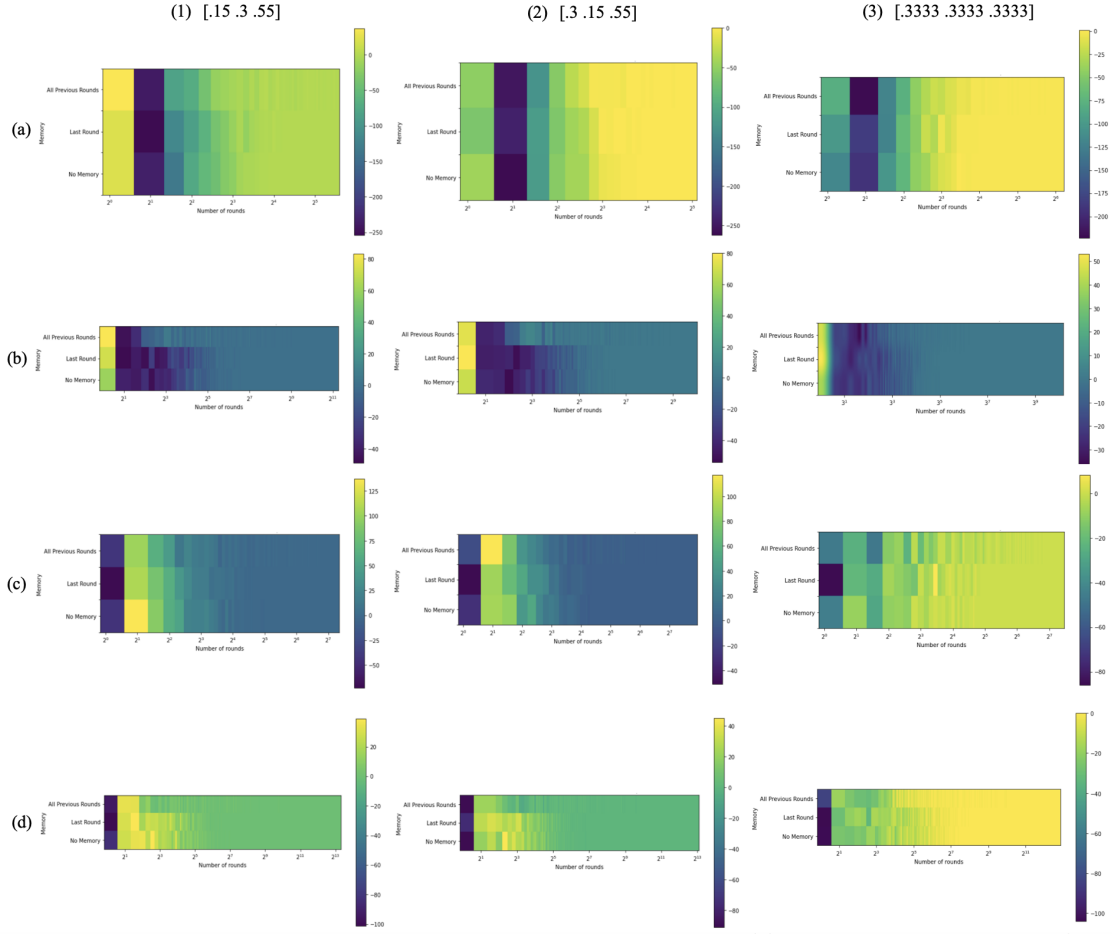


Figure 2.5: Column 1 represents when battlefield payoff distribution is (Laws, Marine Reserves, Community)=(.15 .3 .55). Column 2 represents when battlefield payoff distribution is (Laws, Marine Reserves, Community)=(.3 .15 .55). Column 3 represents when battlefield payoff distribution is even. That is, (Laws, Marine Reserves, Community)=(.3333 .3333 .3333). Row (a) is when the budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)). Row (b) is when the budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)). Row (c) is when the budget for Conservationists is (High, Low, Low)=(20*(People), 10, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)). Row (d) is when the budget for Conservationists is (Low, High, Low)=(1*(People), 200, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)). Negative values represent Poachers winning more games and Positive values represent Conservationists winning more rounds.

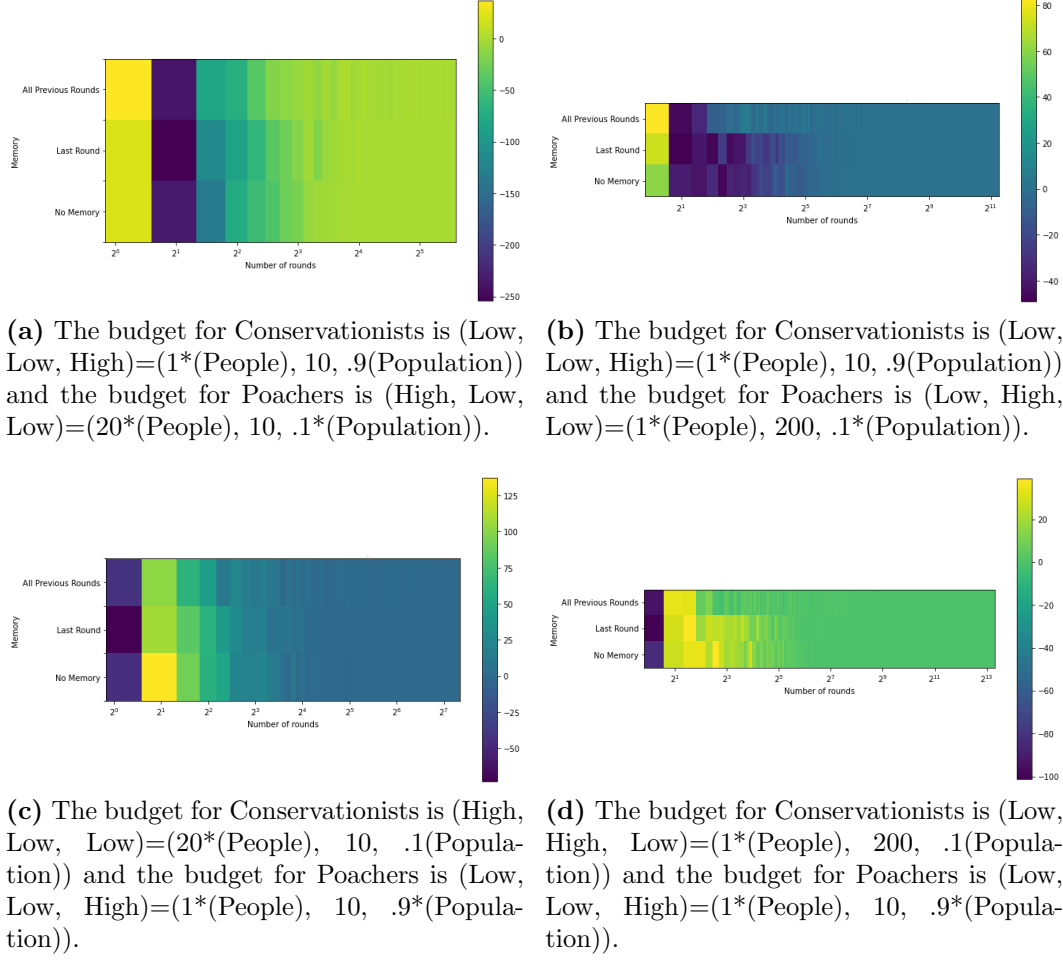
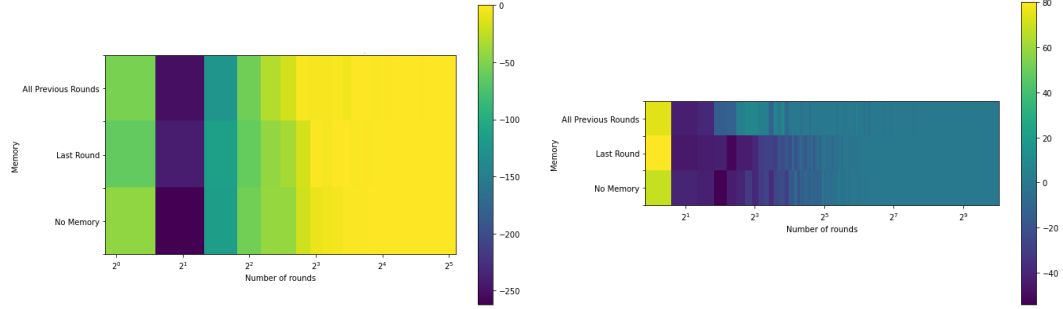
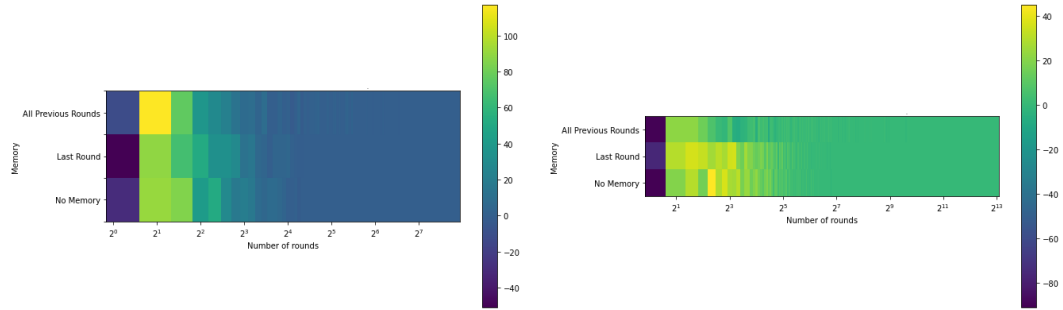


Figure 2.6: Heatmap of the number of games won based on memory and the number of rounds in the game when the payoff distribution is (Laws, Marine Reserves, Community)=(.15 .3 .55). Negative values represent Poachers winning more games and Positive values represent Conservationists winning more rounds.



(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

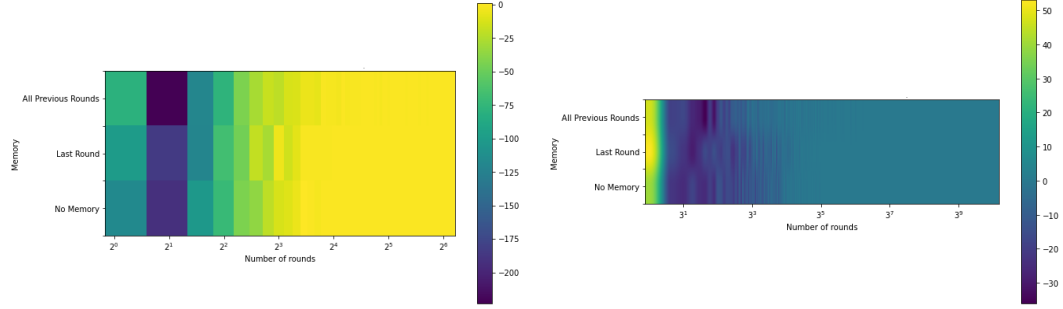
(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).



(c) The budget for Conservationists is (High, Low, Low)=(20*(People), 10, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)).

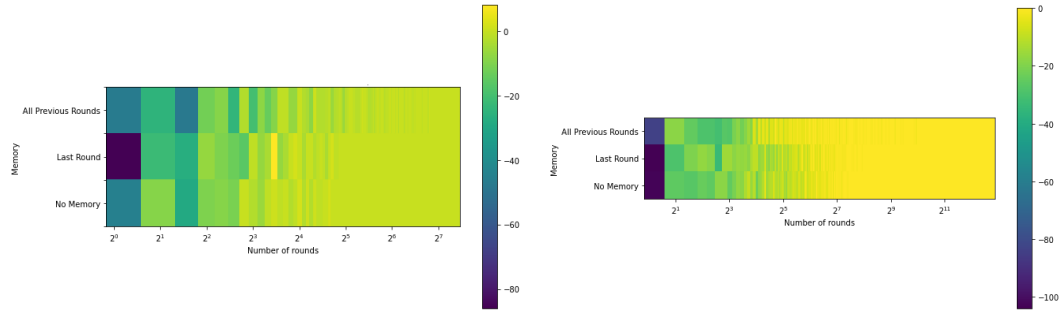
(d) The budget for Conservationists is (Low, High, Low)=(1*(People), 200, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)).

Figure 2.7: Heatmap of the number of games won based on memory and the number of rounds in the game when the payoff distribution is (Laws, Marine Reserves, Community)=(.3 .15 .55). Negative values represent Poachers winning more games and Positive values represent Conservationists winning more rounds.



(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).



(c) The budget for Conservationists is (High, Low, Low)=(20*(People), 10, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)).

(d) The budget for Conservationists is (Low, High, Low)=(1*(People), 200, .1(Population)) and the budget for Poachers is (Low, Low, High)=(1*(People), 10, .9*(Population)).

Figure 2.8: Heatmap of the number of games won based on memory and the number of rounds in the game when the payoff distribution is even ((Laws, Marine Reserves, Community)=(.3333 .3333 .3333)). Negative values represent Poachers winning more games and Positive values represent Conservationists winning more rounds.

games won. The same three different battlefield payoff distributions used in figure 2.1 are considered in figures 2.5 comparisons. That is, one where the the community battlefield holds over half of the payoff bank while the non-monetary battlefield holds twice as much as the monetary battlefield, another where the monetary and non-monetary battlefield switch payoffs, and one where all battlefields have the same distribution. Additionally, the extreme cases of the players' budgets are compared.

Figure 2.5(1) shows when the battlefield payoff vector is [Laws, Marine Reserves, Community]=[.15 .3 .55]. Across memory cases, whoever holds high supporters has the highest chance winning the game if few rounds occur. However, as rounds accumulate, the game favors the opposing player. This makes the first few rounds imperative to the player with low supporters. If Conservationists have high supporters, then they have the most advantage if the game ends in one round with the memory of all previous rounds having the most advantage. Players must choose a strategy that would allow the game to continue to a favorable number of rounds based on their resource distribution. Figure 2.1(1) reveals which strategies could give the high supporter player the best chance of winning by ending the game in few rounds.

The battlefield payoff vector [Laws, Marine Reserves, Community]=[.3 .15 .55] is shown in figure 2.5(2). Again, across memory cases, the player with high supporters has an advantage when round numbers is low. As rounds accumulate, the player with low supporters is favored. If Poachers have high monetary resources and Conservationists have high supporters, then the Poachers only have an advantage with games lasting around 2 rounds. Figure 2.1(2) reveals which strategies could give the high supporter player the best chance of winning by ending the game in few rounds.

Figure 2.5(3) shows scenarios when the battlefields have an even distribution ([Laws, Marine Reserves, Community]=[.3333 .3333 .3333]). Poachers have a significant advantage across memory cases with the ability to ensure winning the game if they have high supporters and Conservationists having high non-monetary resources. Otherwise, the first one or two rounds is the most critical for

Conservationists. When Conservationists have high supporters and Poachers have high non-monetary resources, then Conservationists have the highest likelihood of winning the game across memory cases. However, memory of the last round has the most potential for a favorable outcome. Figure 2.1(3) provides valuable information for strategy selection in an even battlefield scenario.

2.5 Discussion

The goal of this paper is to give insightful information on which strategies could give the desired results relating to illegal fishing using a game theoretic method following the famous Colonel Blotto game framework. Although in the results section, we consider what each player could play to potentially improve their chances of winning the game, here we will only consider what would improve the Conservationists chances of winning and reducing illegal fishing practices. We shift to a bias of Conservationists since our goal is to reduce illegal fishing, bringing concentration to the decisions Conservationists can make to prevail over the Poachers. We present different scenarios where players hold different budget distributions with having a majority of one resource. The resources are monetary, non-monetary, and supporters. We also consider different institutional memory along with different battlefield payoff distributions where the battlefields are laws, marine reserves, and the community. The different memory cases did not have a large effect on the winner distribution, showing that the book keeping or institutional turnover does not impact the long term winner. However, memory does have a large impact of the duration of the game, allowing some games to reach over 4000 rounds. This is due to players repeatedly playing strategies that gave them the most success, so it takes longer for the winner to gain precedence over the other player. Additionally, this could mean that Poachers and Conservationists are locked in an impasse for such an extended period of time, that it would be unreasonable to deem one a winner since other factors such as the

demise of the species, climate change, or societal changes may occur to invalidate the time frame.

The game ends when one player wins the full support of the community. In the model, this is done by one player obtaining all persons as supporters. In application, this means that overall, the community supports either Conservationists or Poachers so drastically that the opposition does not either have the funds or the market to continue their effort. In other words, it is either not feasible for Conservationists to continue to attempt to conserve the species or it is not economic for Poachers to continue the illegal activity.

The most critical battlefield is the community battlefield since the game is over when a player wins the support of the community. However, a player can still win the game even if they start with a low number of supporters. Figure 2.5(1(c),1(d),2(c),2(d)) show that Conservationists can win the game even though they start with a small amount of supporters. This shows that with other resources, players can accumulate supporters.

Regardless of institutional memory, when the battlefield payoff distribution emphasizes the community battlefield, if Conservationists have high monetary resources, then they would most likely prevail over the Poachers if more than one round occurs. This occurs even with few supporters. Tactics could be used that follow strategies such as the ‘Proportional Battlefields’ strategy (figure 2.1(1)-(2)) that would allocate the majority of all resources to the community battlefield. If Conservationists have high non-monetary resources the ‘Even’ or ‘Proportional Battlefield’ strategy would give the best chance of extending the rivalry past one round, hence giving Conservationists an edge. The ‘Even’ strategy allocates all resources evenly across battlefields. If Conservationists have a high number of supporters, they have the highest chance of winning the game if few rounds are played and the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, and ‘Dominant and Community Battlefields’ strategies will give them the highest chance of succeeding in their conservation goals.

The bleakest case for Conservationists is when the battlefields have an even payoff distribution, which can represent a case where laws, marine reserves, and community support are interconnected in such a way that one category does not have significantly more impact on the system as a whole. For example, the community promotes laws for the reduction of poaching along with the creation of marine reserves, laws are made to protect marine reserves, and the public being able to enjoy protected areas further recruits supporters. Regardless of memory, if Conservationists have a high number of supporters, then they have the highest, or only, chance of reducing poaching when the rivalry consists of one round, meaning allocating resources aligning with the ‘Even’, ‘Proportional Battlefields’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategies (figure 2.1(3)) would give the highest chance of Conservationists reaching their conservation goals. If Conservationists have high monetary resources, they have the highest chance of reducing poaching if less than two rounds occur. The ‘Even’, ‘Dominant Two Battlefields’, or ‘Dominant and Community Battlefields’ strategy should be implemented (figure (figure 2.1(3))). If Conservationists have high non-monetary resources, then they will ultimately fail to conserve the species.

Overall, we present information as to which strategies have potential for resulting in desirable outcomes based on the budget of each player. Conversation groups can refer to the results here in choosing the best allocation of their resources according to their resource budget distribution and with supplementation from their region’s emphasized operations. For example, a study was done on the Misool and Kofiau islands comparing the community’s attitude before and after MPA education and outreach programs. It was found that after the programs, more people had positive attitudes towards MPAs [67]. Therefore, for an area such as this, the community battlefield would contribute a large payoff and budget allocation should reflect that.

2.6 Future Work

In this paper, we focus on battlefields corresponding to laws, marine reserves, and community influence. However, the methods presented here could be extended to include other battlefield categories such as patrolling or enforcement. Although, the categories in this paper cover the enforcement of the laws and reserved areas, creating a new battlefield could emphasize the effort it would take. For example, in Mexico, intensive beach management including beach patrolling has had a significant positive impact on sea turtle nesting sites [42].

Additionally, players have a budget consisting of monetary, non-monetary, and supporter resources. The non-monetary resources could be broken into more specific categories such as boats and nets. This could provide more information about if targeting a specific equipment category could impact conservation efforts. Also, allowing new equipment to be made or destroyed could change the dynamics of the game. However, equipment such as boats can vary greatly. For example, in the Philippines, fishing boats can be municipal or commercial boats, which each consist of subcategories, furthering the difference between the different types [2]. Standardizing across the different equipment would have to occur for proper comparisons.

The time it takes for allocation to different battlefields to have an effect on conservation efforts would also be a valuable addition. Laws can be made fairly quickly while the time it takes to change the attitude of the community may take considerably longer. Within community education programs, methods such as surveys should be used throughout the program such as when insecticide-treated bed nets were implemented in Kenya. Surveys revealed mothers' concerns and gave researchers potential areas for consideration and targeted education [74]. Knowing the community is key when implementing an outreach program, but takes time and consideration

Although this model is made specifically for marine applications, it could easily be adapted to different conservation scenarios. Elephant and Rhino poaching in Africa is a large issue due to ivory trade. Elephant poaching has been on an upward

trend, and although elephants do not currently have the highest level of protection, budget allocation could help plan which strategy would result in most favorable results for conservation [50]. Additionally, rhino conservation face obstacles such as “inadequate funding and law enforcement, weak policy and legal frameworks, and disgruntled and marginalized communities who antagonize conservation efforts, illegal harvesting and international trade, and habitat fragmentation and loss” [20]. Considering different budget allocation strategies would help Conservationists make a more informed approach to give the rhino a better chance at survival.

2.7 Conclusion

In this paper, we present how to allocate a budget to reduce illegal fishing. We use a game theoretic approach with a basis of the famous Blotto Game in which players allocate resource across different battlefields to win the most payoff. We present three different battlefields: laws, marine reserves, and community. The players’ budgets also consist of different resources including monetary, non-monetary, and supporter resources. Each player allocates their resources by choosing one of nine strategies in the hopes of winning the most payoff possible and ultimately reaching their conservation goals or their goal of the continuation of poaching practices. The game capturing this rivalry consists of a series of rounds with different starting budgets per round, reflecting the outcome of the previous round. The game is over once a player wins the support of the entire community, meaning that either Conservationists or Poachers have lost either the funds or market to continue their effort. Different institutional memory scenarios are explored, corresponding to different bookkeeping diligence and turnover rates, as well as different battlefield payoff distributions.

In summary, we found that even if a player starts disadvantaged they can still succeed in their conservation or poaching goals. For example, if Conservationist starts with limited supporter resources, when the community battlefield has the most contribution, they can still succeed in conserving the targeted species. Additionally,

with some budget distributions, the first few rounds is crucial if the player hopes to succeed. Lastly, if battlefields have an even payoff distribution, the Conservationists have an unfortunately low probability of prevailing over the Poachers, especially as the game consists of more rounds. This could be because when battlefields have equal payoff and Conservationists either have high monetary or supporter resources, they can win over enough supporters at the beginning to win the game due to either not having to win over much more of the community to have full support or to have enough monetary resources to effectively promote their cause. However, as the rounds progress and Poachers win supporters over, Conservationists lose their advantage and are unable to gain it back since the community battlefield does not hold the majority payoff. Ultimately, the combination of the players' initial budgets and battlefield payoff distribution is what allows one player to have an advantage over their opponent.

Memory does not have a sizable affect on who wins the round, but can affect the duration of the rivalry with “memory of all previous rounds” producing the longest encounters. Overall, we present results than could aid Conservationists in choosing strategies to fight against Poachers by giving different scenarios of battlefield payoff distributions, institutional memory, and player budget distributions. Although specific case-by-case information is vital to every conservation effort, the model presented here can help make a more informed decision.

Appendix

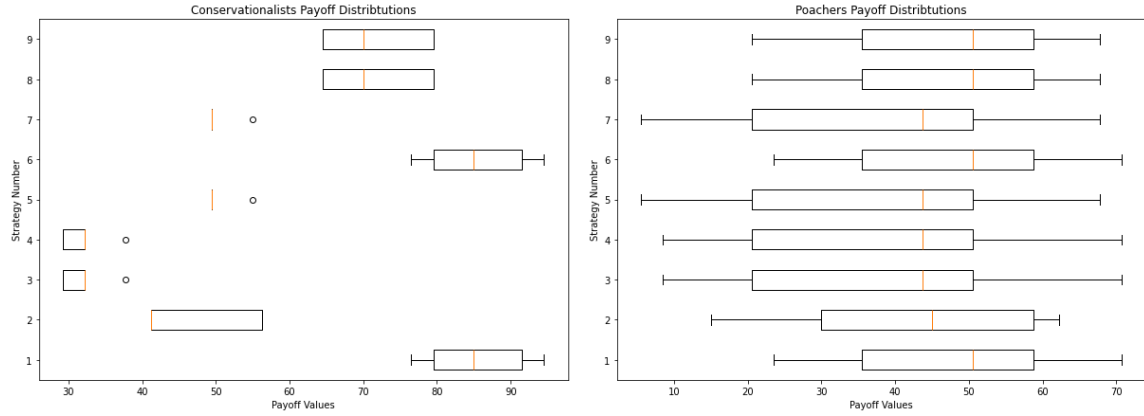


Figure 2.9: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.15 .3 .55], meaning that the community contributed the most with more than half of the payoff bank while the marine reserves contributed a moderate amount and laws contributed the least. The resources for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] while the resources for Poachers is [Low, High, Low]=[1*(People), 200, .1*(Population)]. If Conservationists play strategies 1, 6, 8, or 9 they will win regardless of which strategy Poachers play. However, strategies 1 and 6 have a higher median payoff. No strategy will guarantee Poachers will win, but strategies 1, 6, 8, and 9 have relatively the same median payoff that would win the round.

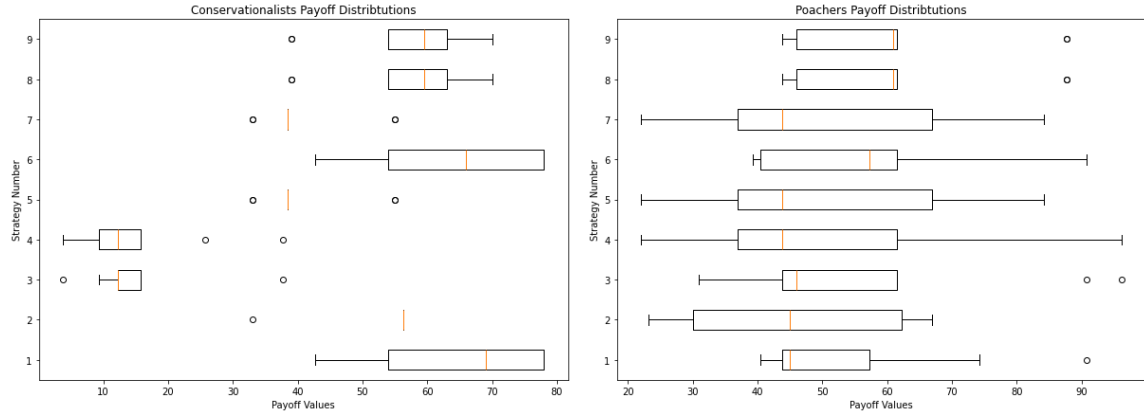


Figure 2.10: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.15 .3 .55], meaning that the community contributed the most with more than half of the payoff bank while the marine reserves contributed a moderate amount and laws contributed the least. The resources for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] while the resources for Poachers is [High, Low, Low]=[20*(People), 10, .1*(Population)]. If Conservationists play strategies 2, 6, 8, or 9 they have a high chance of winning the most payoff. However, strategies 1 has the highest median payoff. No strategy will guarantee Poachers will win, but strategies 8 and 9 have the same median payoff that would win the round.

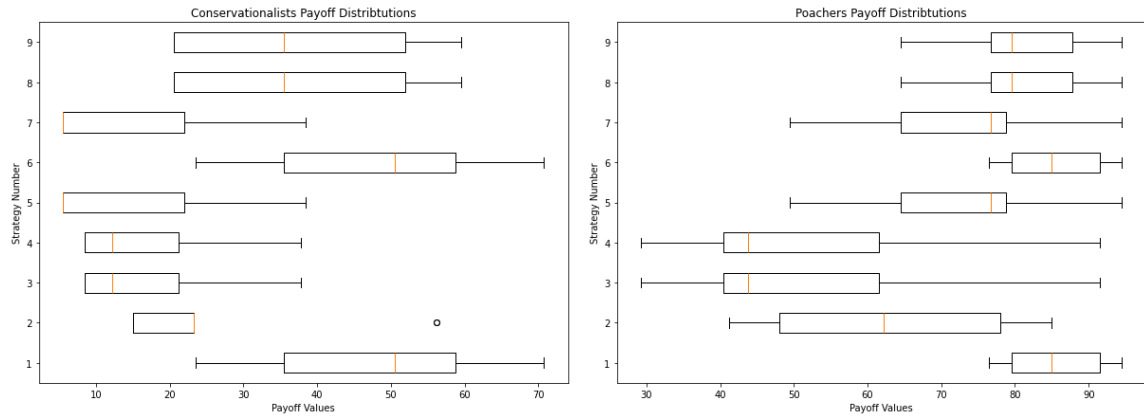


Figure 2.11: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.15 .3 .55], meaning that the community contributed the most with more than half of the payoff bank while the marine reserves contributed a moderate amount and laws contributed the least. The resources for Conservationists is [Low, High, Low]=[1*(People), 200, .1(Population)] while the resources for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win, but strategies 1 and 6 have the approximately the same median payoff that would win the round. If Poachers play strategies 1, 6, 8, or 9 they will win the most payoff. However, strategies 1 and 6 has the highest median payoff.

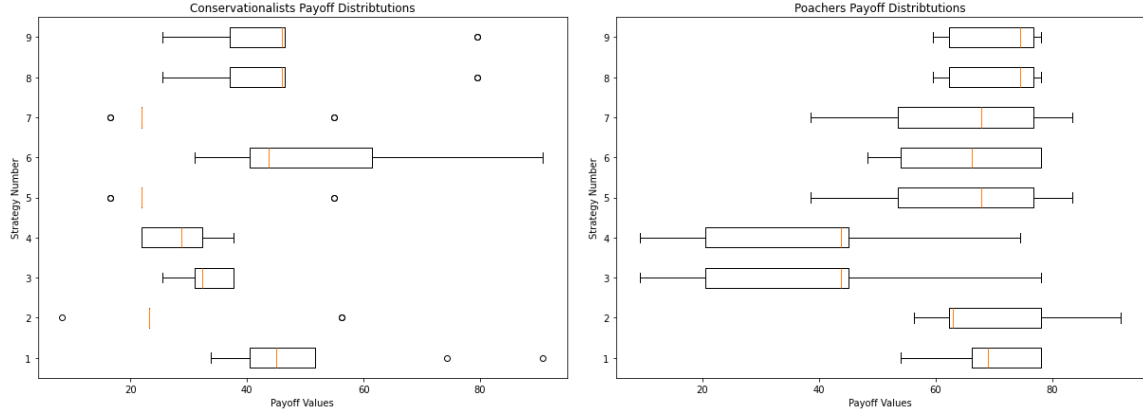


Figure 2.12: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.15 .3 .55], meaning that the community contributed the most with more than half of the payoff bank while the marine reserves contributed a moderate amount and laws contributed the least. The resources for Conservationists is [High, Low, Low]=[20*(People), 10, .1(Population)] while the resources for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win. However, strategy 6 has the highest chance of giving Conservationists a winning payoff. If Poachers play strategies 1, 2, 8, or 9 they will win the most payoff. However, strategies 8 and 9 has the highest median payoff.

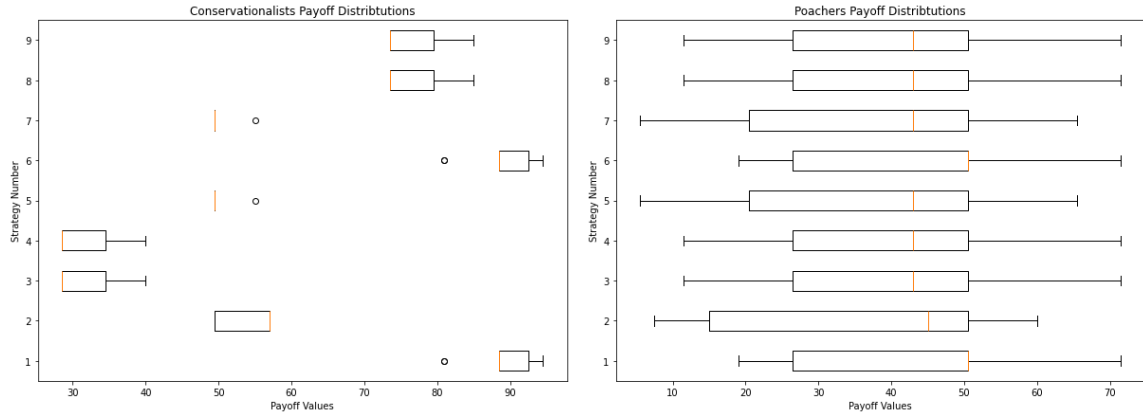


Figure 2.13: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3 .15 .55], meaning that the community contributed the most with more than half of the payoff bank while the laws contributed a moderate amount and marine reserves contributed the least. The budget for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] and the budget for Poachers is [Low, High, Low]=[1*(People), 200, .1*(Population)]. If Conservationists play strategies 1, 6, 8, or 9 they will win the most payoff. However, strategies 1 and 6 has the highest median payoff. No strategy will guarantee Poachers will win. However, strategies 1 and 6 have the highest median payoff that wins the round.

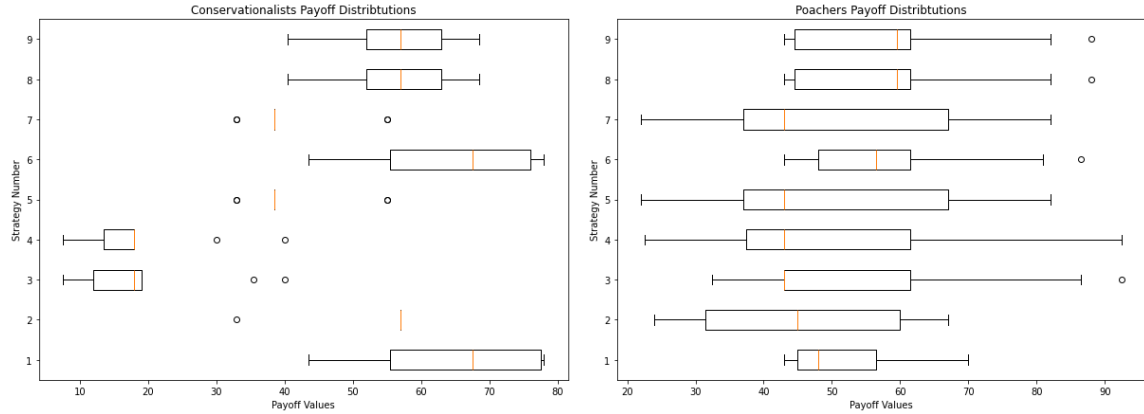


Figure 2.14: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3 .15 .55], meaning that the community contributed the most with more than half of the payoff bank while the laws contributed a moderate amount and marine reserves contributed the least. The budget for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] and the budget for Poachers is [High, Low, Low]=[20*(People), 10, .1*(Population)]. No strategy will guarantee Conservationists will win. However, strategies 1, 2, 6, 8, and 9 has the highest chance of giving Conservationists a winning payoff. Additionally, no strategy will guarantee Poachers will win the round, but strategies 8 and 9 give poachers the highest chance of winning and the highest median payoff.

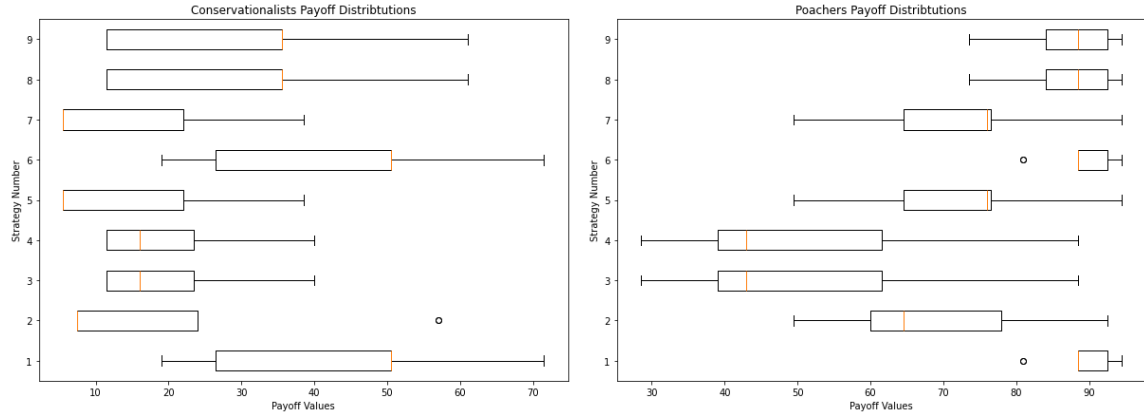


Figure 2.15: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3 .15 .55], meaning that the community contributed the most with more than half of the payoff bank while the laws contributed a moderate amount and marine reserves contributed the least. The budget for Conservationists is [Low, High, Low]=[1*(People), 200, .1(Population)] and the budget for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win. However, strategies 1 and 6 has the highest chance of giving Conservationists a winning payoff and the highest median payoff. If Poachers play strategies 1, 6, 8, or 9 they will win the most payoff.

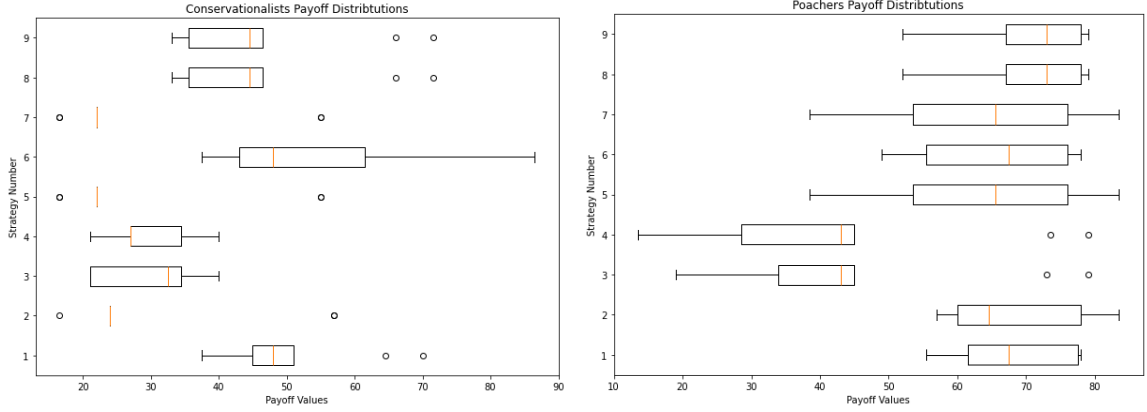


Figure 2.16: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3 .15 .55], meaning that the community contributed the most with more than half of the payoff bank while the laws contributed a moderate amount and marine reserves contributed the least. The budget for Conservationists is [High, Low, Low]=[20*(People), 10, .1(Population)] and the budget for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win. However, strategy 6 has the highest chance of giving Conservationists a winning payoff. If Poachers play strategies 1, 2, 8, or 9 they will win the most payoff. However, strategies 8 and 9 has the highest median payoff.

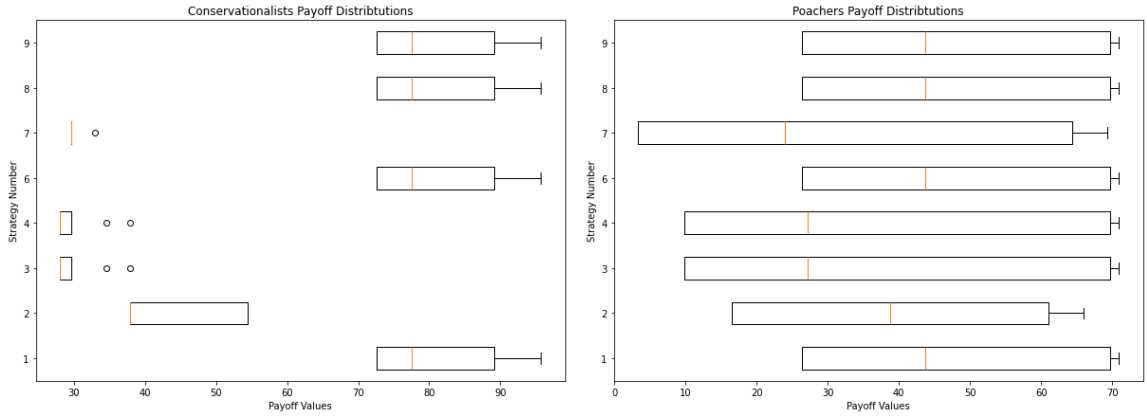


Figure 2.17: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3333 .3333 .3333], meaning that all battlefields contribute equal amounts of the Payoff Bank. Strategy 5 has been omitted due to the inability to pay it with the case of equal battlefields. The budget for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] and the budget for Poachers: [Low, High, Low]=[1*(People), 200, .1*(Population)]. If Conservationists play strategies 1, 6, 8, or 9 they will win the most payoff with all having the same median payoff. No strategy will guarantee Poachers will win. However, strategies 1, 6, 8, and 9 has the highest chance of giving Poachers a winning payoff.

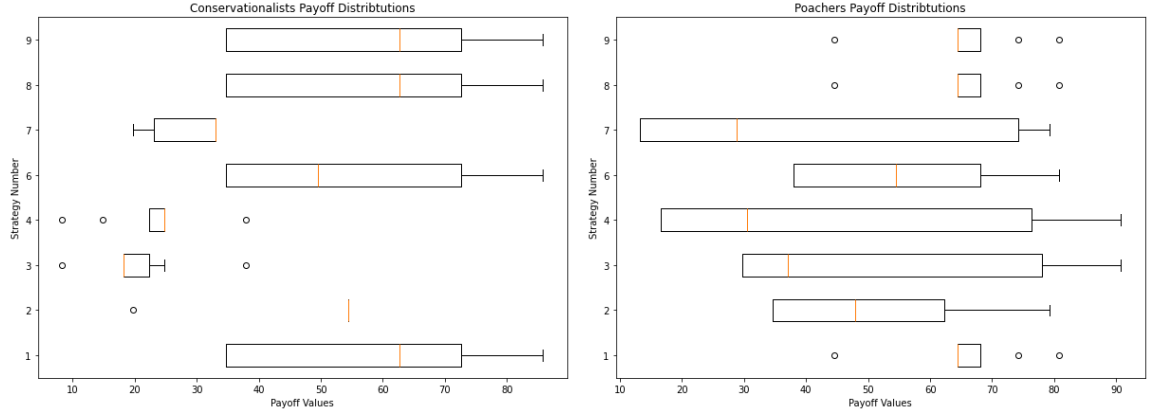


Figure 2.18: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3333 .3333 .3333], meaning that all battlefields contribute equal amounts of the Payoff Bank. Strategy 5 has been omitted due to the inability to pay it with the case of equal battlefields. The budget for Conservationists is [Low, Low, High]=[1*(People), 10, .9(Population)] and the budget for Poachers is [High, Low, Low]=[20*(People), 10, .1*(Population)]. No strategy will guarantee Conservationists will win. However, strategies 1, 6, 8, and 9 has the highest chance of giving Conservationists a winning payoff. Additionally, no strategy will guarantee Poachers will win the round, but strategies 1, 8 and 9 give poachers a very high chance of winning and the highest median payoff.

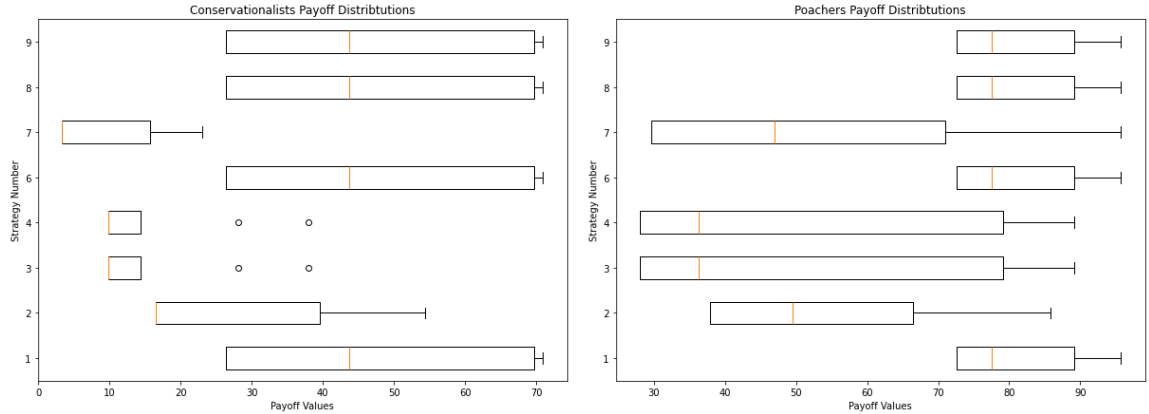


Figure 2.19: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3333 .3333 .3333], meaning that all battlefields contribute equal amounts of the Payoff Bank. Strategy 5 has been omitted due to the inability to pay it with the case of equal battlefields. The budget for Conservationists is [Low, High, Low]=[1*(People), 200, .1(Population)] and the budget for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win. However, strategies 1, 6, 8, and 9 has the highest chance of giving Conservationists a winning payoff. If Poachers play strategies 1, 6, 8, or 9 they will win the most payoff with all having the same median payoff.

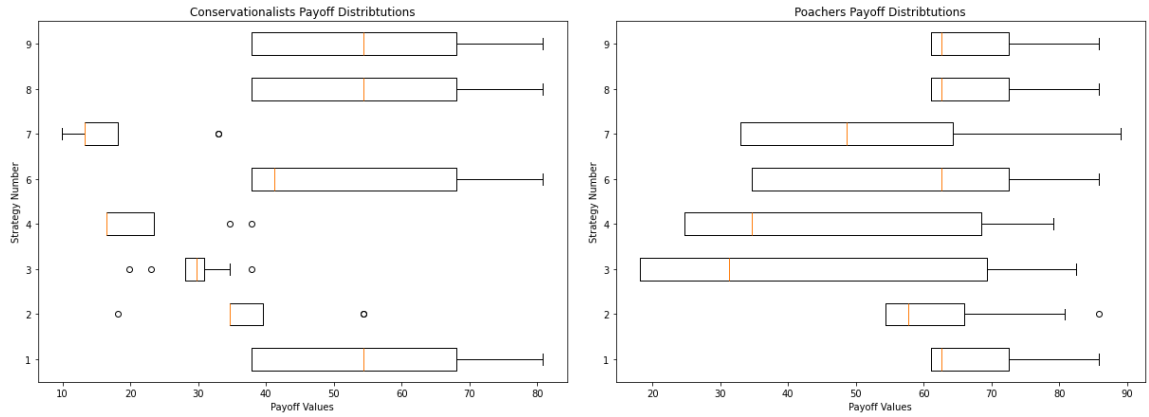
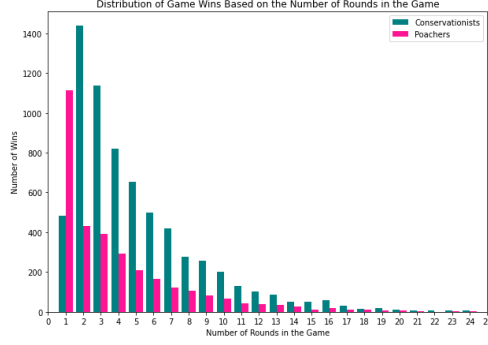
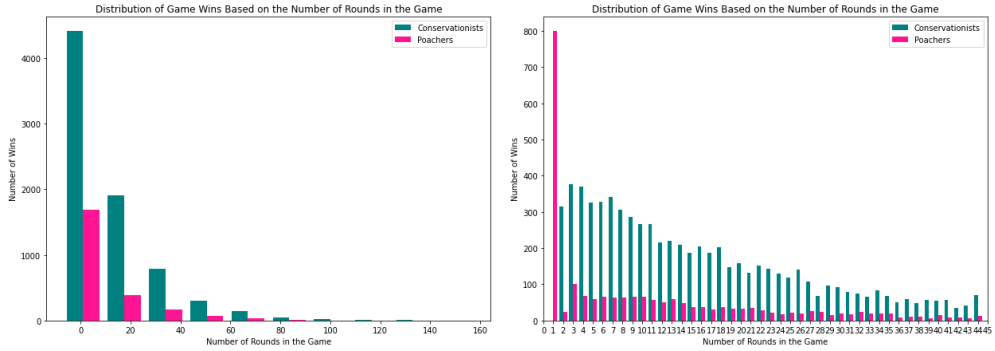


Figure 2.20: The battlefield payoff vector is [Laws, Marine Reserves, Community]=[.3333 .3333 .3333], meaning that all battlefields contribute equal amounts of the Payoff Bank. Strategy 5 has been omitted due to the inability to pay it with the case of equal battlefields. The budget for Conservationists is [High, Low, Low]=[20*(People), 10, .1(Population)] and the budget for Poachers is [Low, Low, High]=[1*(People), 10, .9*(Population)]. No strategy will guarantee Conservationists will win. However, strategies 1, 6, 8, and 9 has the highest chance of giving Conservationists a winning payoff. If Poachers play strategies 1, 2, 8, or 9 they will win the most payoff. However, strategy 2 has a lower median payoff that strategies 1, 8, and 9.

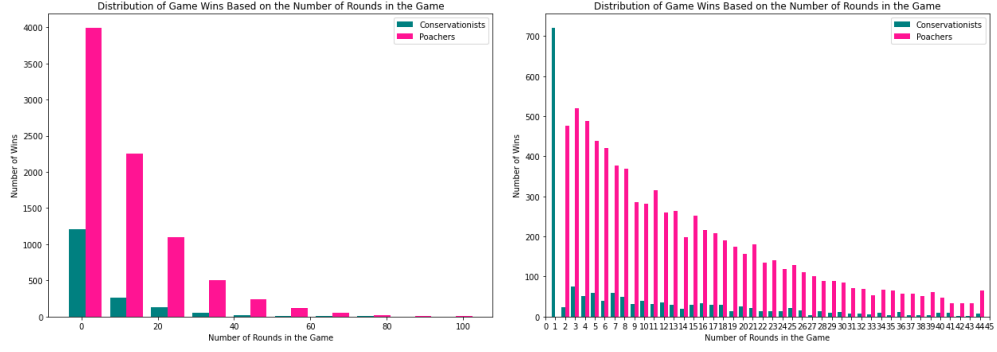


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, 10, $.1 \times (\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10, $.9 \times (\text{Population})$).

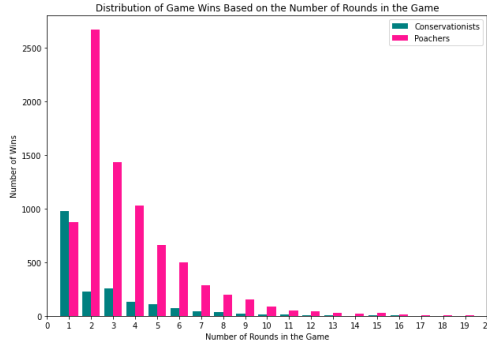


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, 200, $.1 \times (\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10, $.9 \times (\text{Population})$).

Figure 2.21: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[$.15$ $.30$ $.55$] and Poachers having a high number of supporters.

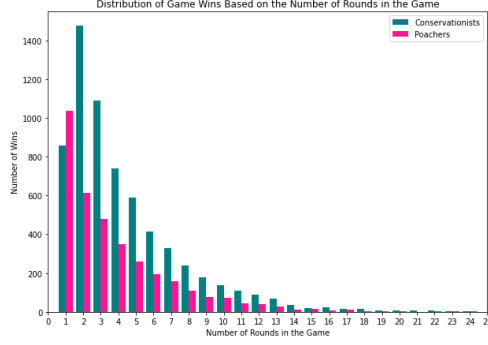


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

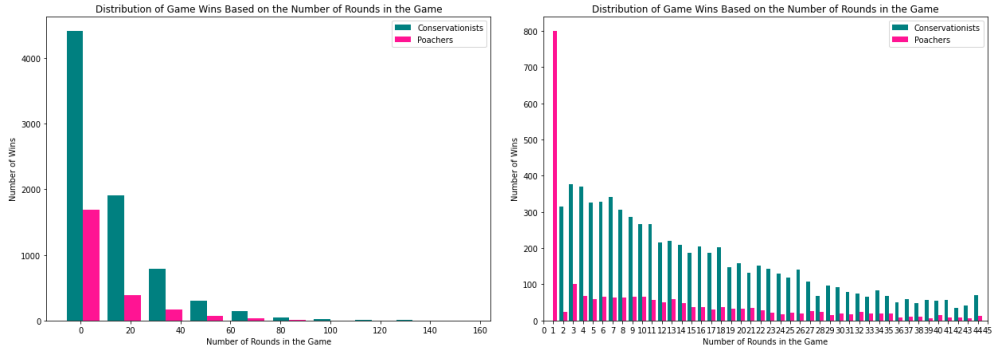


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.22: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.15 .30 .55] and Conservationists having a high number of supporters.

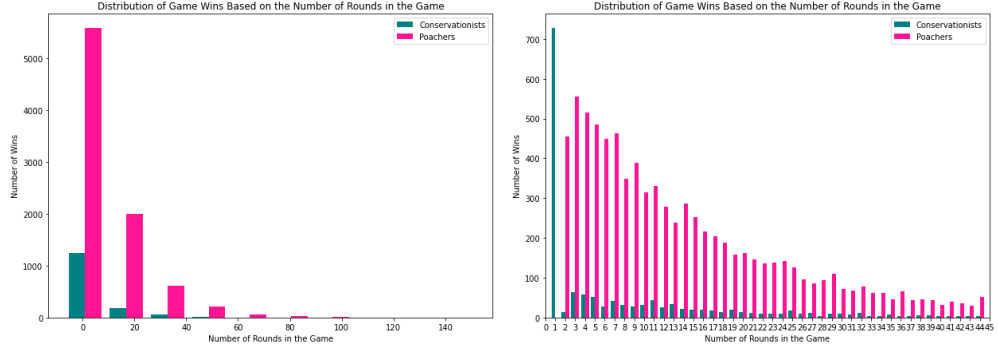


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, $10 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9(\text{Population})$).

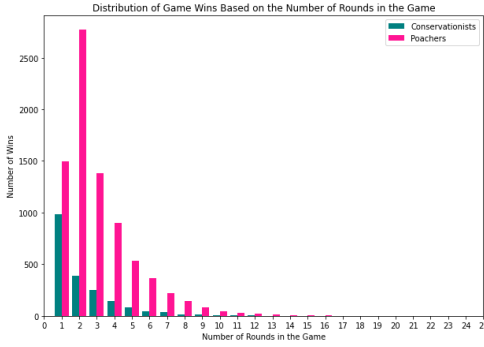


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, $200 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9(\text{Population})$).

Figure 2.23: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[$.30 \ .15 \ .55$] and Poachers having a high number of supporters.

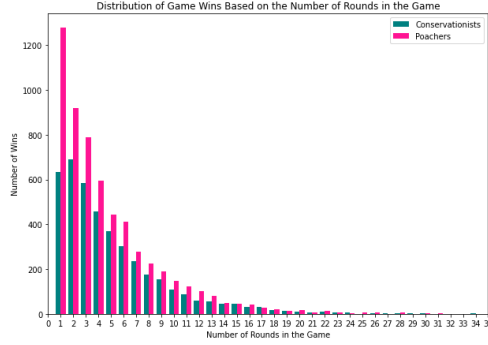


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

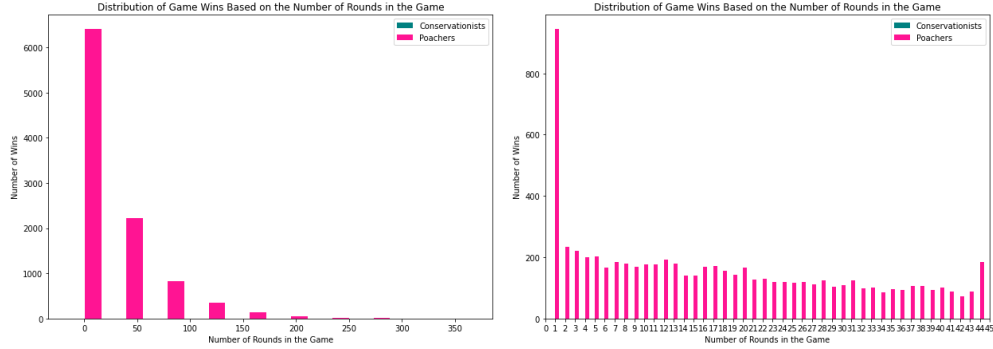


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.24: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.30 .15 .55] Conservationists having a high number of supporters.

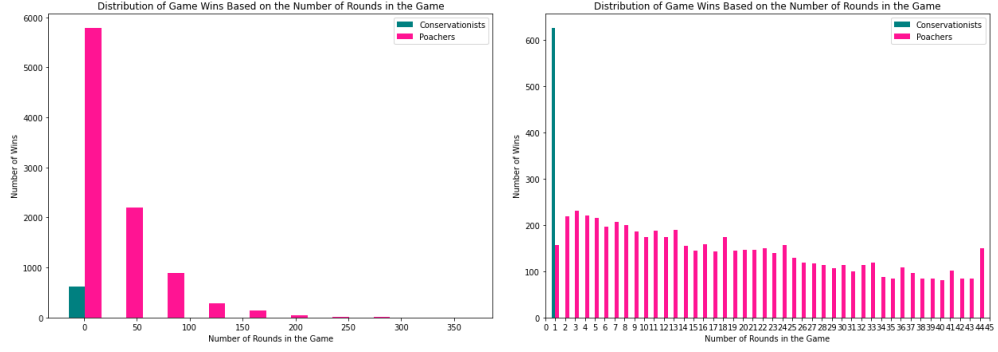


(a) The budget for Conservationists is (High, Low, Low)=($20 * (\text{People})$, $10, .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 * (\text{People})$, $10, .9 * (\text{Population})$).

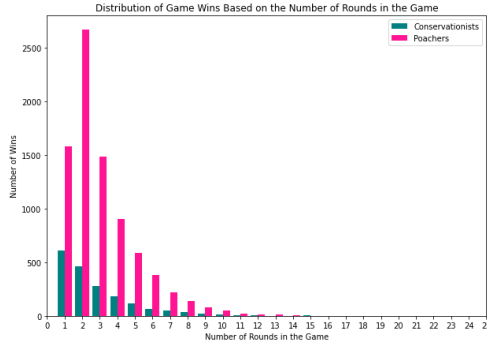


(b) The budget for Conservationists is (Low, High, Low)=($1 * (\text{People})$, $200, .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 * (\text{People})$, $10, .9 * (\text{Population})$).

Figure 2.25: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Poachers having a high number of supporters.

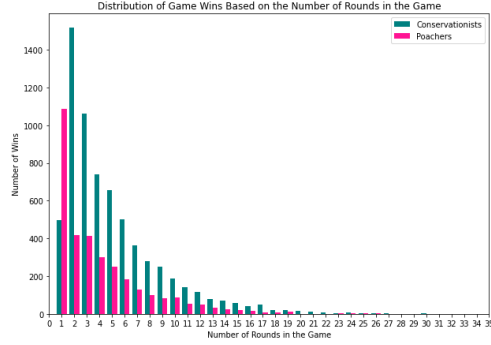


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

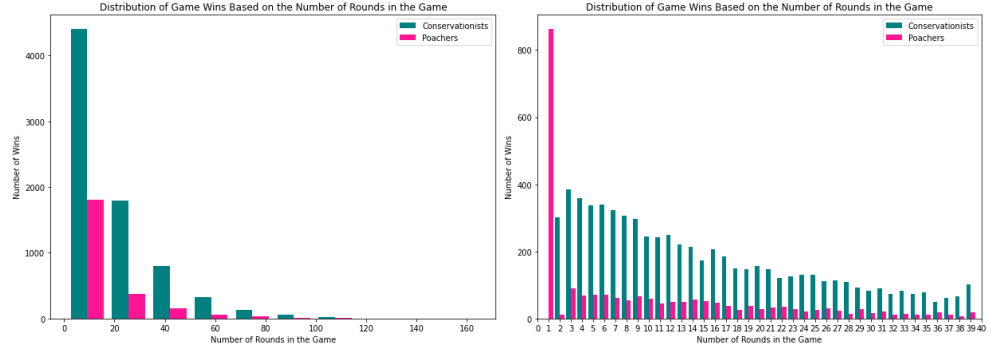


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.26: No memory with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Conservationists having a high number of supporters.

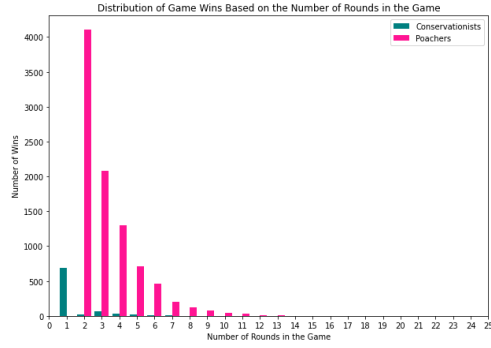


(a) The budget for Conservationists is (High, Low, Low)=($20 * (\text{People})$, $10, .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 * (\text{People})$, $10, .9 * (\text{Population})$).

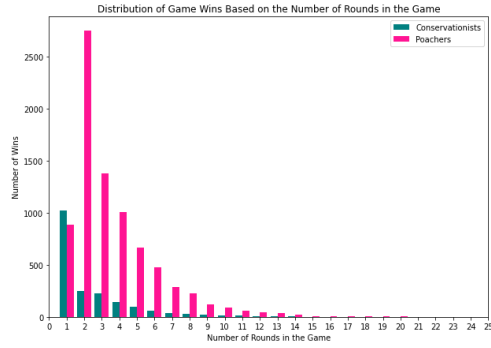


(b) The budget for Conservationists is (Low, High, Low)=($1 * (\text{People})$, $200, .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 * (\text{People})$, $10, .9 * (\text{Population})$).

Figure 2.27: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[$.15 \ .30 \ .55$] and Poachers having a high number of supporters

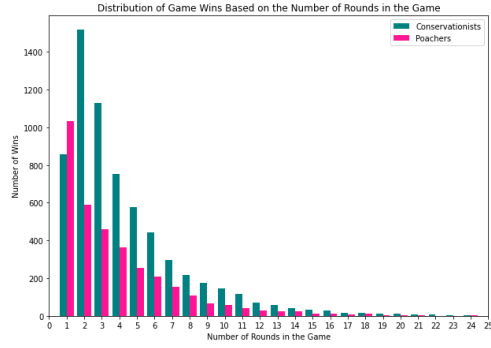


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

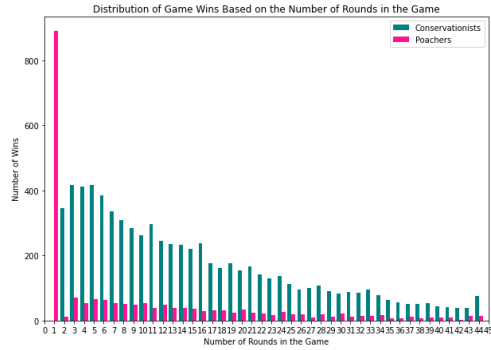


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.28: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.15 .30 .55] and Conservationists having a high number of supporters

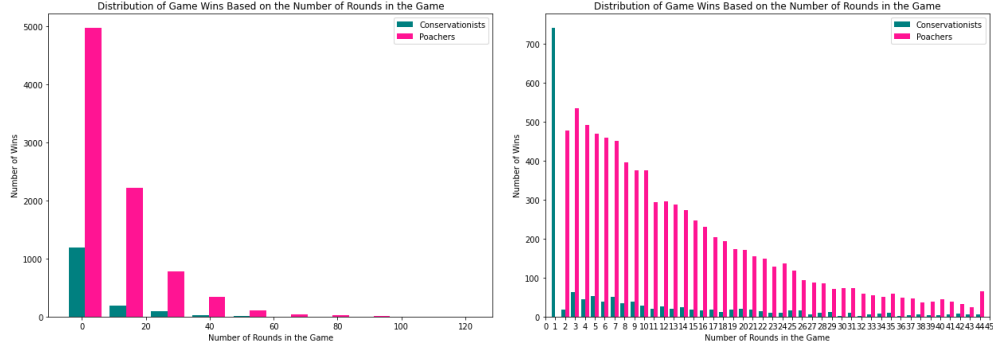


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, 10 , $.1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10 , $.9 \times (\text{Population})$).

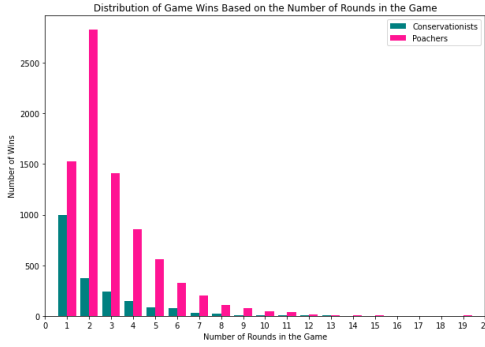


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, 200 , $.1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10 , $.9 \times (\text{Population})$).

Figure 2.29: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.30 .15 .55] Poachers having a high number of supporters.

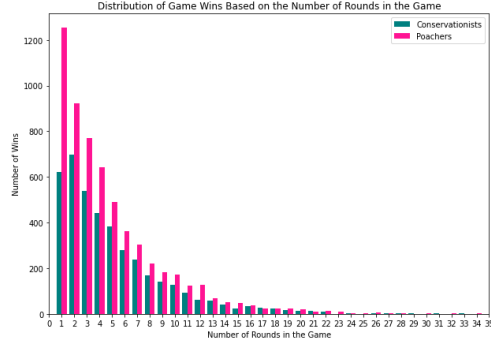


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

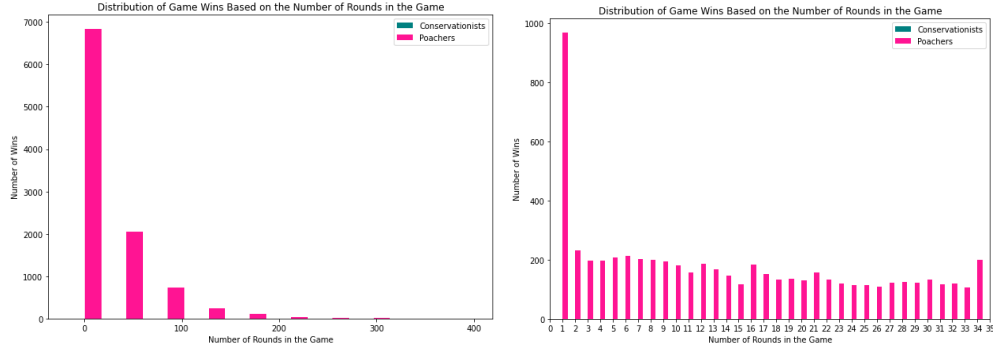


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.30: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.30 .15 .55] and Conservationists having a high number of supporters.

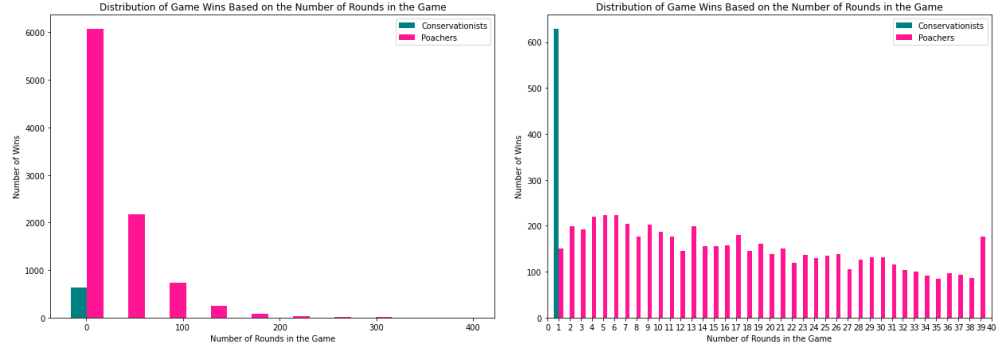


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, $10 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$).

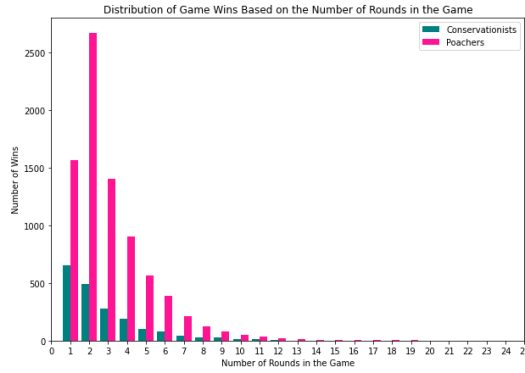


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, $200 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$).

Figure 2.31: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Poachers having a high number of supporters.

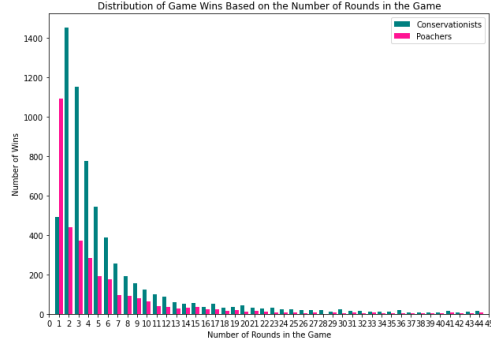


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

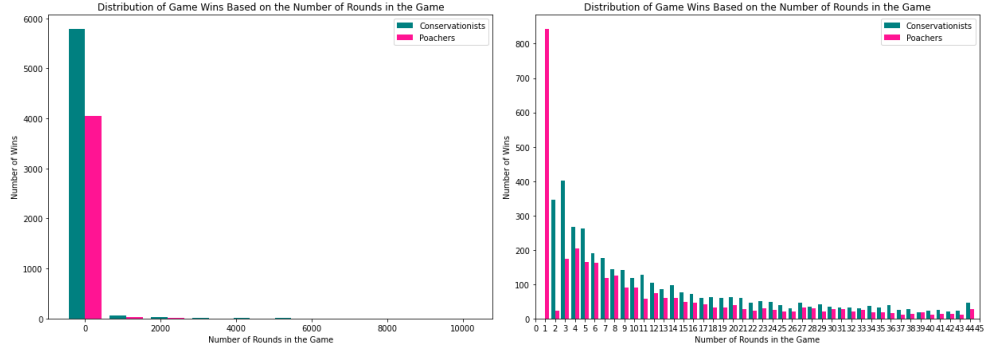


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.32: Memory of last round with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Conservationists having a high number of supporters.

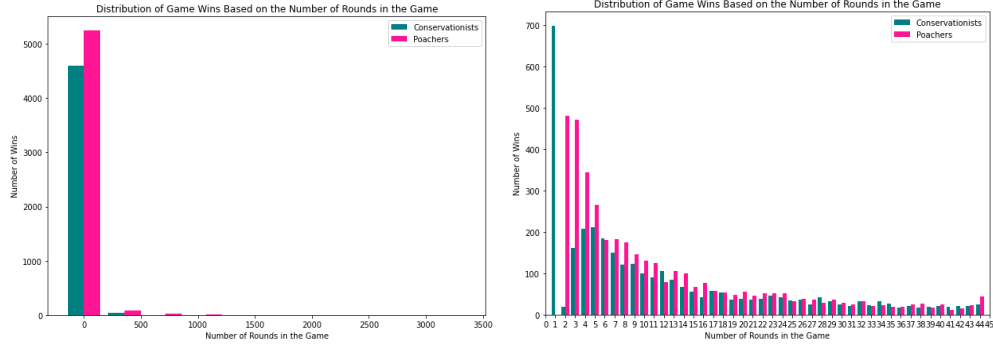


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, $10 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$).

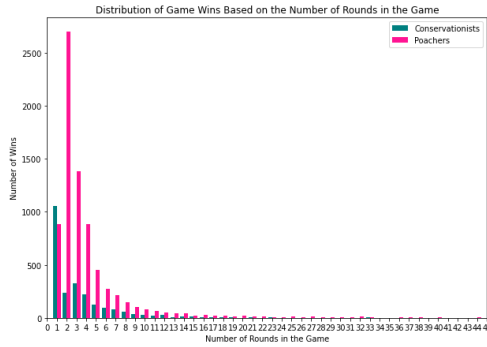


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, $200 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$).

Figure 2.33: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.15 .30 .55] and Poachers having a high number of supporters.

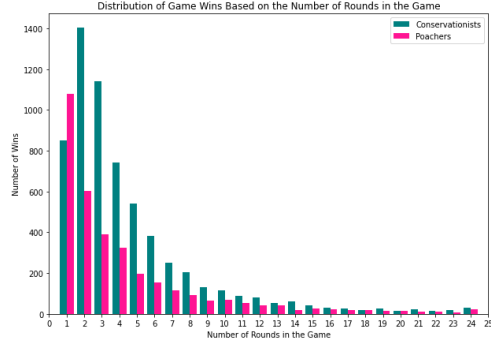


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

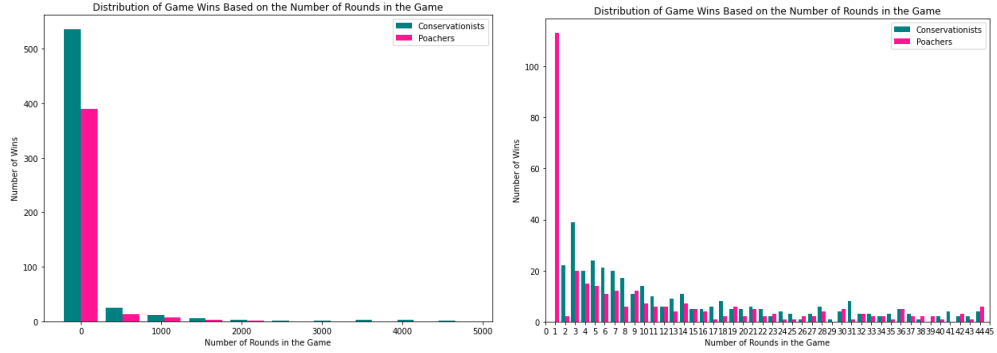


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.34: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.15 .30 .55] and Conservationists having a high number of supporters.

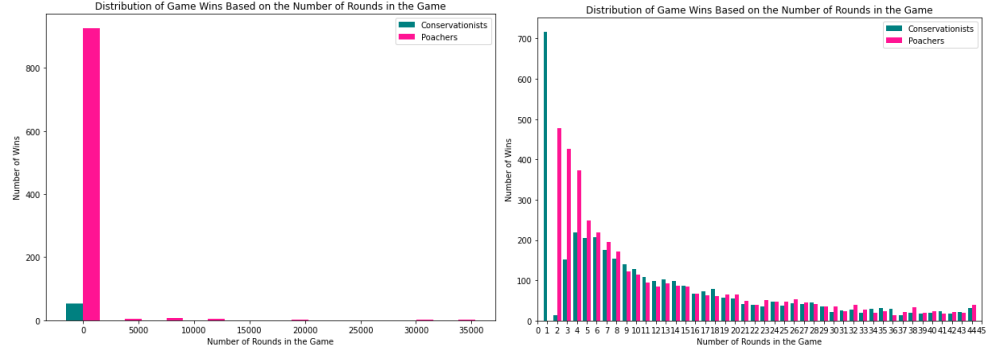


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, $10 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$).

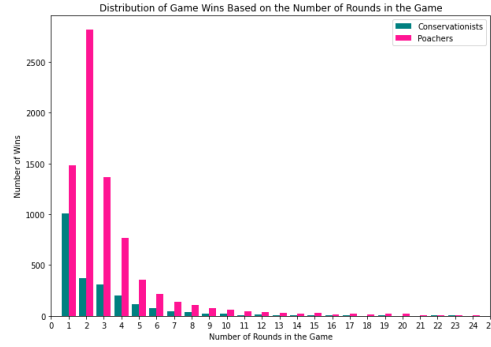


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, $200 \times .1(\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, $10 \times .9 \times (\text{Population})$). 1000 games were played instead of 10,000 due to run time

Figure 2.35: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.30 .15 .55] and Poachers having a high number of supporters.

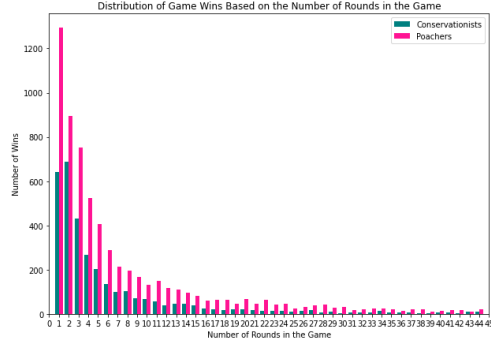


(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).

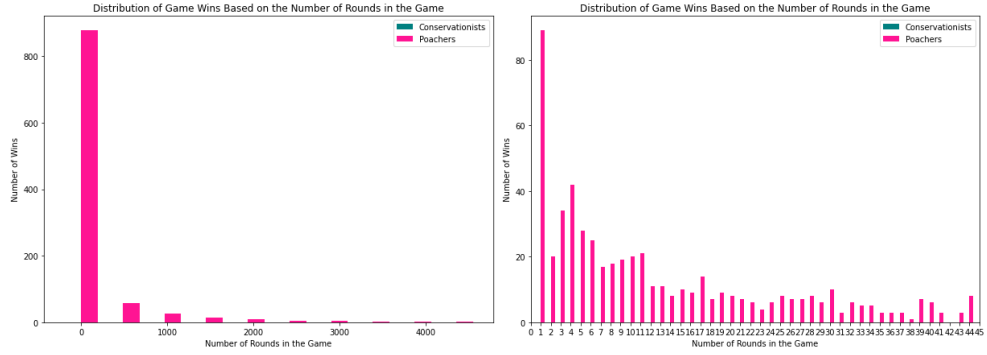


(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)).

Figure 2.36: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.30 .15 .55] and Conservationists having a high number of supporters

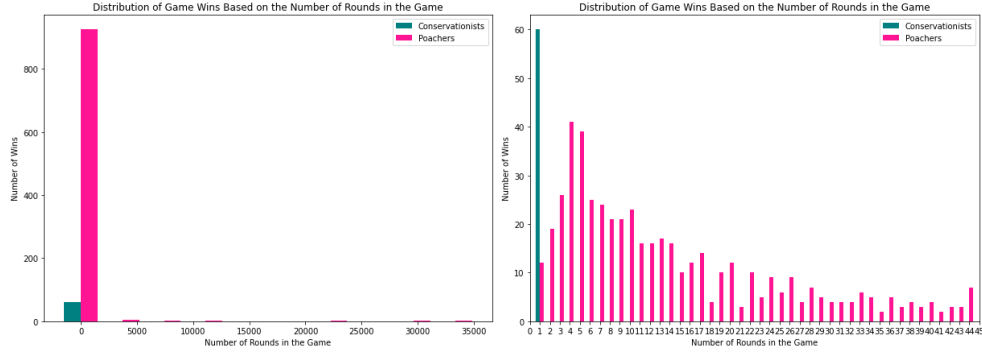


(a) The budget for Conservationists is (High, Low, Low)=($20 \times (\text{People})$, 10, $.1 \times (\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10, $.9 \times (\text{Population})$).

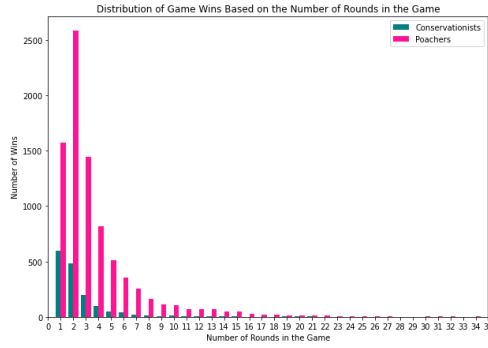


(b) The budget for Conservationists is (Low, High, Low)=($1 \times (\text{People})$, 200, $.1 \times (\text{Population})$) and the budget for Poachers is (Low, Low, High)=($1 \times (\text{People})$, 10, $.9 \times (\text{Population})$). 1000 games were played instead of 10,000 due to run time

Figure 2.37: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Poachers having a high number of supporters.



(a) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (Low, High, Low)=(1*(People), 200, .1*(Population)).



(b) The budget for Conservationists is (Low, Low, High)=(1*(People), 10, .9(Population)) and the budget for Poachers is (High, Low, Low)=(20*(People), 10, .1*(Population)). 1000 games were played instead of 10,000 due to run time.

Figure 2.38: Memory of all previous rounds with the battlefield payoff distribution being [Laws, Marine Reserves, Community]=[.3333 .3333 .3333] and Conservationists having a high number of supporters.

Chapter 3

Reactive Scope Model with Multiple Mediators and an Energy Budget

3.1 Abstract

Recent advances in understanding of the animal stress response have extended traditional theories of homeostasis into a conceptual framework of reactive scope: a more nuanced theory that contextualizes an animal’s capacity to respond to stressors based on their physiological state and life history. Over the past 15 years, empirical investigation into the validity of reactive scope as an explanatory framework has led to further critical and novel insights. More recent work presented a quantitative and predictive model of the reactive scope framework [118]. Building on this first quantitative characterization, we extend the quantitative model with the addition of an energy budget, or reservoir, and allow multiple different mediators to pull from such budget. Multiple mediators being considered simultaneously provides a more realistic representation for how an animal could reach homeostatic overload and allows a more nuanced and accurate quantitative prediction of outcomes from exposures to stressors over time. Additionally, we explore the sensitivity of predictions of health state to the choice of rate parameters, focusing on the decline and recovery of threshold functions. Coupling stress event magnitude and duration yields interesting results in how stress event parameters affect when and how long a mediator spends in detrimental stress states, with one interesting result being that a shorter duration can have negative affects in comparison to a longer duration.

3.2 Introduction

Definitions of the psychological, physiological, and behavioral responses to stressors as “an animal’s stress response” have ranged from Claude Bernard’s ‘milieu intérieur’ (or ‘internal environment’) [53] to the more recent concepts of homeostasis and allostasis [99]. Homeostasis maintains stability within an animal’s biological system by regulating variables such as hormone levels, chemical levels, or physiological functionality [21]. Homeostasis can be interrupted by “stress”, a process which can

be described by a framework involving the following elements: stressful stimulus, stressor, stress response, and stress effect [70]. Here, stress is defined as the homeostatic state being challenged and a stress response follows in response to compensate and maintain homeostasis [70]. An example of a stress response is a flight-or-fight reaction [10]. However, less obvious indications such as cortisol or temperature changes can also signal a stress response. In contrast to the assumption of constant baseline value posited by homeostasis, allostasis instead considers a variable baseline value [70]. This allows for natural variation due, for example, to daily or seasonal fluctuations. However, extended periods of time of experiencing stress can lead to increased allostatic load, contributing to negative psychological and physiological effects [101]. Research around allostasis shows that allostatic overload can induce neuroendocrine, cardiovascular, and emotional responses which can lead to a compromised immune systems along with other bodily functions, further leading to disease or poor health [112].

There are several indicators or mediators of a stress response. Some of these include physical responses such as changes in heart rate, temperature, or blood pressure. However, steroid hormone levels, such as that of cortisol and corticosterone, are used frequently as stress indicators due to their rapid response to stress changes [84, 82]. Increases in hormone levels have been shown to improve performance during short term stress events, such as hunting or mating, but extended durations at elevated levels can lead to negative effects [82].

Different studies use different stressors to induce a response. Exercise has been used to induce stress in test subjects, such as forced time on a treadmill or participating in swimming activities [123]. Other experimentally manipulated stressors include food restriction and isolation [121]. Isolation can affect the psychological state of the animal and also trigger stress responses [36]. We build on the a previous model by [118], which in turn relied on and reflected experimental results on wild birds through invoking stress response mediators presented in [35, 13]

Mathematical models have been used in both psychology and physiology to provide novel insights into stress dynamics and make concrete predictions for validation and hypothesis generation. Such models have included stress responses and homeostasis [43, 37, 99, 35], allostasis [109], and allostatic overload along with steroid hormone tracking to measure stress responses [76]. Mathematical models involving allostasis and stress responses can provide predictive guidance to determine stress thresholds and how stress exposure can affect an animal’s internal functions, behavior, and evolutionary success. Models involving an animal’s energy budget have considered how the animal utilizes energy from food throughout life history events such as growth, reproduction, and general maintenance [86]. We here review and build upon the model designed by [118], adding the capability to consider multiple mediators simultaneously and introducing an energy budget, which provides limitations for the animal that is affected by the mediators.

3.3 Review of previous Reactive Scope paper

Recent work by [118] introduced a quantitative formulation of the reactive scope conceptual model first presented in [99]. (Note: In describing the model on which we build, we quote directly from the description of the equations and parameter definitions given in [118] both for clarity and consistency in notation throughout this section.) In that formulation, stress impacts physiological mediators such as changes in behavior, glucocorticoids, antibody titers, and heart rate. These mediators can then fall into a set of states that correspond to the animal’s ability to withstand the stressor challenge: predictive homeostasis, reactive homeostasis, homeostatic overload, and homeostatic failure (see Figure 3.1).

A critical aspect of the reactive scope model and quantitative formulation is the inclusion of ‘wear and tear’, which is defined as “the sizes of the ranges associated with each classification can change temporarily or permanently in response to stress events” [118]. As a mediator reaches homeostatic overload, the ability for an animal to

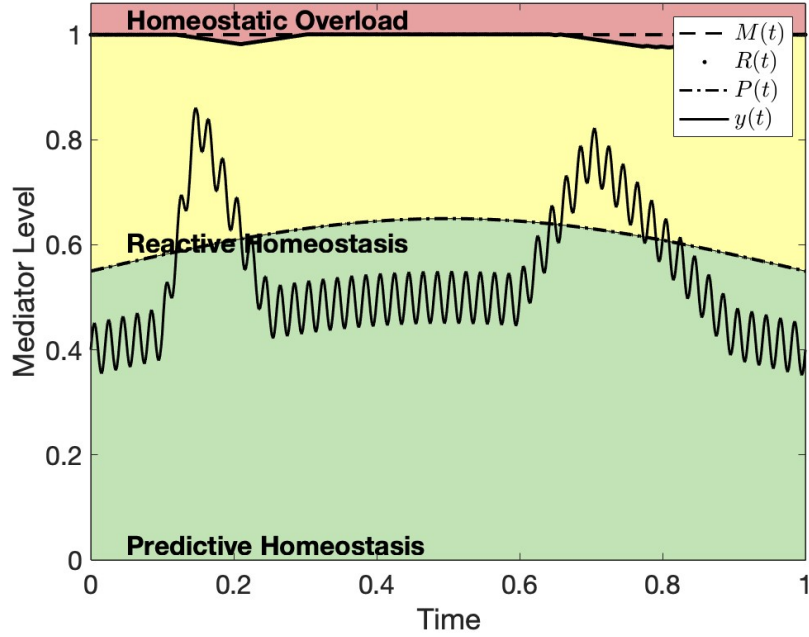


Figure 3.1: The predictive homeostasis range is for normal activity levels such as foraging or seasonal stresses. The reactive homeostasis range is when a stress event causes the mediator to reach non-routine levels, but are low enough that the animal can still recover enough to avoid hitting the next category, homeostatic overload. However, if a mediator reaches that level, then the animal starts to reflect a compromised state. Homeostatic failure is when an animal can not longer regulate the mediator at a normal level and is depicted by [118] and [99] as being below the predictive homeostasis range. The threshold for predictive homeostasis range is denoted $P(t)$ and the threshold for homeostasis overload is denoted $R(t)$. We will adopt the same notation in the additions this paper provides.

withstand stress decreases, causing the threshold for entry into homeostatic overload to decrease, allowing the animal to enter homeostatic overload faster and more frequently in subsequent stress events.

In [118], stress events were described using the following equation

$$s(t) = \sum_{i=1}^n s_i \psi_{\mu_i, \sigma_i}(t) \quad (3.1)$$

where n is the number of stress events being considered, s_i is the magnitude of the stress response for the i th stress event, ψ_{μ_i, σ_i} is a function that captures the desired behavior of the stress event (e.g. up- and down-regulation time, increase and decrease rates, etc.), and μ and σ are parameters that dictate the time and duration of the event. Three different functions are presented and compared for ψ_{μ_i, σ_i} . To capture the mediator values under a stress event, the equation

$$y(t) = a_s \sin(b_s t) + a_c \sin(b_c t) + s(t) + y_c \quad (3.2)$$

is formulated where a_s and a_c are the amplitude of seasonal and circadian variation respectively, b_s and b_c are period of seasonal and circadian variation respectively, and y_c is the basal level of the physiological mediator. $R(t)$ and $P(t)$ are the threshold curves between reactive homeostasis and homeostatic overload and predictive homeostasis range and reactive homeostasis range respectively. The term $M(t)$ was introduced to represent the maximum value that $R(t)$ could recover to at the conclusion of a stress event. $P(t)$ is denoted:

$$P(t) = a_s \sin(b_s t) + a_c + y_c + y_{act} \quad (3.3)$$

where y_{act} represents changes in mediator level due to predictable activity. Putting everything together, the model presented is the following:

$$\frac{dM}{dt} = -r_1\theta(y(t) - R(t)) \quad (3.4)$$

$$\frac{dR}{dt} = -r_2\theta(y(t) - P(t)) + r_3\theta(P(t) - y(t))\theta(M(t) - R(t)) \quad (3.5)$$

with $\theta(x)$ representing the Heaviside function presented below.

$$\theta(x) = \begin{cases} 0 & x \leq 0 \\ 1 & x > 0 \end{cases}$$

The mediator must be in either the reactive homeostasis or homeostatic overload ranges, $y(t) > P(t)$, in order for $R(t)$ or $M(t)$ to change. $R(t)$ will only decrease while $y(t) > P(t)$ and $M(t)$ will only decrease while $y(t) > R(t)$. It was also found that duration and intensity of the stress event can have a significant impact on the threshold curves. For example, a stress event that has a lower intensity but a far longer duration can lead to homeostatic overload, while a short stress event at a high intensity could not induce homeostatic overload.

Overall, [118] created the first quantitative formulation of the conceptual reactive scope model and provided different functions for the threshold curves. Analysis revealed how different parameters could affect an animal avoiding or entering homeostatic overload.

3.4 Expansions on Prior Work

We present two additions to the previous reactive scope model presented by [118]. The first is that we allow multiple mediators to be considered simultaneously. The other is the introduction of the concept of an energy budget. This allows for each

mediator to claim a portion of the available energy. We achieve these expansions by building off of equations (3.4) and (3.5) with θ remaining the Heaviside function.

In order to consider multiple mediators, we altered the equations (3.4) and (3.5) to intake a vector $\vec{y} = \{y_1(t), y_2(t), \dots, y_n(t)\}$. Each of the $y_i(t)$ terms represent different mediators that are driven by stress events, allowing each mediator to respond independently, including the potential for differential dependence on circadian or seasonal variation and other biological factors. Therefore the equations become

$$\begin{aligned}\frac{dM_i}{dt} &= -r_{1,i}\theta(y_i(t) - R_i(t)) \\ \frac{dR_i}{dt} &= -r_{2,i}\theta(y_i(t) - P_i(t)) + r_{3,i}\theta(P_i(t) - y_i(t))\theta(M_i(t) - R_i(t))\end{aligned}\tag{3.6}$$

which considers n different mediators, with each mediator having its respective system.

The equations are modified further with the consideration of an energy budget. First we define a few terms: $E(t)$ represents the energy budget/reservoir which will be drawn upon by different mediators and can be replenished over time; $A(t)$ is an energy acquirement and maintenance function that describes an animal's energy use in the absence of stress (*i.e.*, net baseline energy use); and α_i allows for proportional depletion, depending on the amount by which the respective mediator surpassed the predictive range. Adding in the energy budget, the equations become

$$\begin{aligned}\frac{dM_i}{dt} &= -r_{1,i}\theta(y_i(t) - R_i(t)) \\ \frac{dR_i}{dt} &= -\rho(E)r_{2,i}\theta(y_i(t) - P_i(t)) + r_{3,i}\theta(P_i(t) - y_i(t))\theta(M_i(t) - R_i(t))\end{aligned}\tag{3.7}$$

where $\rho(E) = C_i + (c_i - C_i)e^{-E}$ and C_i and c_i are appropriate constants that maintain the psychological impacts stress has on an animal's mediators. There are a few critical required properties involving these constants for the $\rho(E)$ function. First, $\rho(E) \rightarrow C_i$ as $E \rightarrow \infty$, which prevents even an infinite amount of spare energy from stopping the decrease of $R(t)$. Second, $\rho(E) \rightarrow c_i$ as $E \rightarrow 0$, which prevents the rate of decline of

$R(t)$ from increasing without bound as the energy budget is diminished. The change in the energy budget as n mediators reduces it becomes

$$\frac{dE}{dt} = A(t) - \sum_{i=1}^n \alpha_i (y_i(t) - P_i(t)) \theta(y_i(t) - P_i(t)) \quad (3.8)$$

In implementation, we chose $A(t) = k \sin(2\pi nt)$ where n is the number of oscillations you expect over the time period and k is the amplitude of the oscillations. We set $\alpha_i = 1$ for all i , but, in real world application, this should change with species-specific knowledge about mediator prominence.

3.5 Analysis of Expanded Model

We consider a few scenarios of the energy budget model compared with the original model. Note that for the introduction of an energy budget along with multiple mediators and in keeping with [118], all mediators have equivalent rate parameters ($r_1 = r_2 = r_3$). We also assume the following mediator parameters are the same across mediators: years = 1, period of seasonal variation (b_s) = π , period of circadian variation and (b_c) = $50(2\pi)$, and the basal level (y_c)=0.4. However, mediator parameter amplitude of seasonal (a_s) variation and amplitude of circadian variation (a_c) vary across mediators. To analyze the impact of the expansions of the model, we contrast the outcomes of exposure to two stress events under different scenarios.

The two biggest impacts on the energy budget are the duration and magnitude of the stress events (see Figure 3.2). In row (2), predictably, the first stress event causes the energy budget to drop marginally, but the second stress event, which has a higher magnitude, causes a more significant decrease. In row (3), we see a steady decline in the energy budget starting when both mediators break into homeostatic overload with the first stress event. The energy budget has an increased rate of decline when

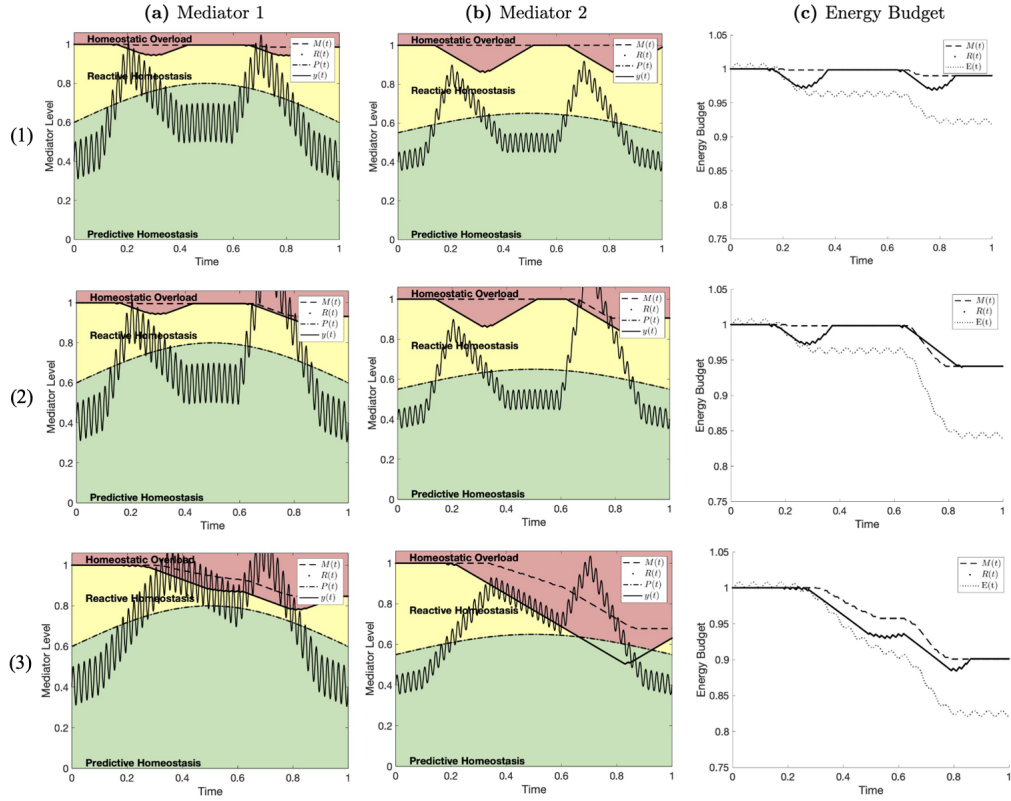


Figure 3.2: In (1), two stress events occurred, each with a magnitude of 0.4 and a duration of 0.1. (a) Represents the first mediator with parameter values $a_s = 0.2$, $a_c = 0.1$, and $r_1 = r_2 = r_3 = 0.5$. Notice that homeostatic overload is reached in both stress events. (b) Represents the second mediator with parameter values $a_s = 0.1$, $a_c = 0.05$, $r_1 = r_2 = r_3 = 0.8$. Neither stress event reaches homeostatic overload. (c) Represents the Energy Budget. As in [118], $M(t)$ represents the maximum value that $R(t)$ can recover to at the conclusion of a stress event and $R(t)$ is the threshold for homeostatic overload. $E(t)$ represents the Energy Budget, which decreases due the first and second stress events, along with $M(t)$ and $R(t)$.

In (2), the two mediators have the same parameters as in 3.1. However, the stressors' magnitudes (s_i) differs. The magnitude of the first stressor is 0.4 while the the magnitude of the second stressor is 0.7. (a) is the effect the two stressors have on the first mediator. (b) is the effect the two stressors have on the second mediator. (c) is the effect the mediators' response had on the energy budget.

In (3), the two mediators have the same parameters as 3.1. However, the stressors' duration (σ_i) differs. (a) is the effect two stressors with duration 0.25 and 0.1 respectively have on the first mediator. (b) is the effect two stressors with duration 0.25 and 0.1 respectively have on the second mediator. (c) is the effect the mediators' response had on the energy budget. Note that in this scenario the second stressor starts before the first stressor has completely ended.

the second stress event starts, which pushes both mediators back into homeostatic overload. However, the first event did not completely finish before the second stress event started, meaning the energy budget is always in a state of decline once it starts decreasing. This shows the relationship our model captures between duration of a stress event and the dynamics in their impact: the decline of the animal's energy budget, especially in the absence of any recovery period between stress events.

3.6 Parameter Analysis

In order to provide more insight into the dynamics of the system causing a mediator to reach the reactive homeostasis and homeostatic overload ranges, as well as the time spent in these ranges, we consider the effect each r_i value has on the system by the effect they have on the functions $M(t)$ and $R(t)$. We also consider the scenario in which the duration of a stress event is a function of the magnitude (by either a scalar or exponential relationship). This shows how the coupling between duration and magnitude affects the length of time a mediator spends in the reactive homeostasis and homeostatic overload ranges.

Staying consistent with the constraints presented in [118], r_1 , r_2 , and r_3 are all strictly positive and $r_1 \leq r_2$. $R(t) \leq M(t)$ for all t , $R(t)$ should decrease temporarily if $P(t) < y(t) < R(t)$, should decrease permanently if $y(t) > R(t)$, and increases to $M(t)$ when $y(t) < P(t)$. Further, $M(t)$ decreases permanently when $y(t) > R(t)$. r_1 is the rate of decrease of $M(t)$ when $y(t) > R(t)$. r_2 is the rate of decrease of $R(t)$ when $y(t) > P(t)$. r_3 is the rate of recovery of $R(t)$ when $y(t) < P(t)$ and $R(t) < M(t)$. Changing the r_i parameters does not change the $y(t)$ function, but does change the times and severity of reaching the reactive homeostasis and homeostatic overload ranges. We consider six different variations of r_i (Figure 3.3 (2)-(7)) values and compare them to $r_1 = r_2 = r_3 = 0.5$ (Figure 3.3 (1)). We chose $r_1 = r_2 = r_3$ to stay consistent with [118] in the comparison case. When r_1 is set at a small value,

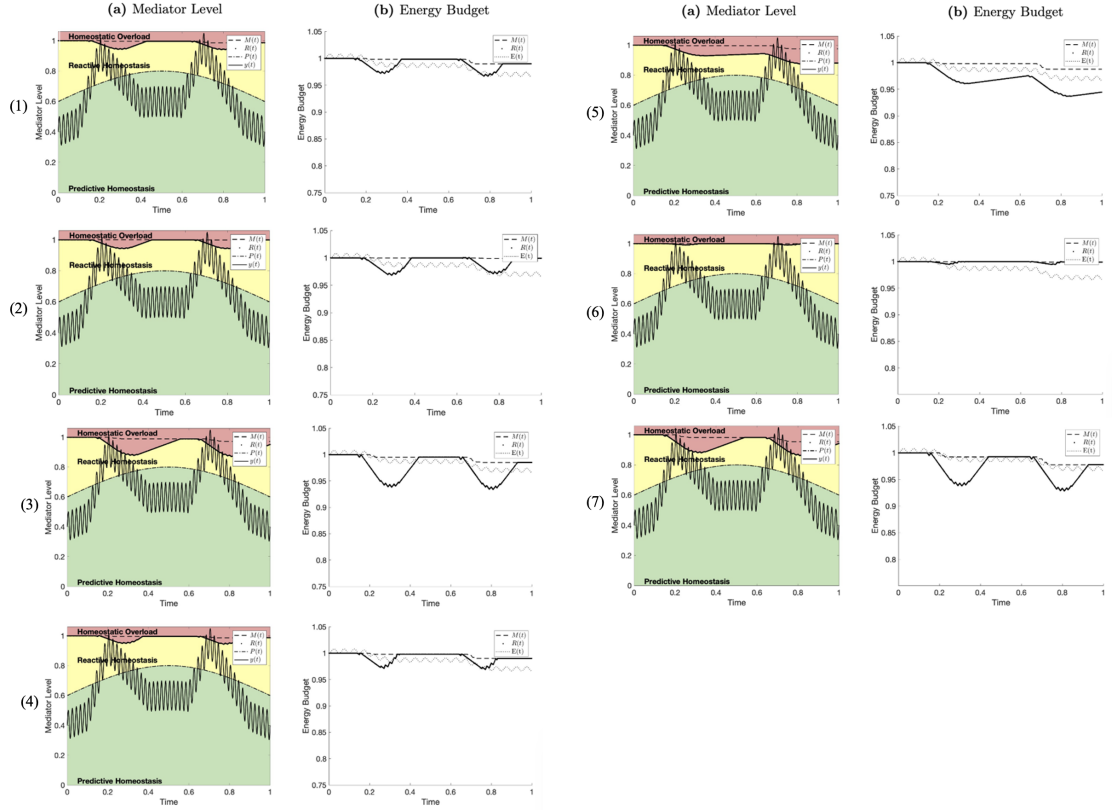


Figure 3.3: In (1), we consider the same parameters as Figure 3.2 (1a). That is $r_1 = r_2 = r_3 = 0.5$ with both stress events having a magnitude (s_i) of 0.4 and duration (σ_i) of 0.1. We will use this Figure as a comparison for (2)-(7). In (2), $r_1 = 0.05$ while $r_2 = r_3 = 0.5$. In (3), $r_2 = 0.95$ while $r_1 = r_3 = 0.5$. In (4), $r_3 = 0.95$ while $r_1 = r_2 = 0.5$. In (5), $r_3 = 0.05$ while $r_1 = r_2 = 0.5$. In (6), $r_1 = 0.05$, $r_2 = 0.1$, and $r_3 = 0.5$. In (7), $r_1 = 0.75$, $r_2 = 0.95$, and $r_3 = 0.5$.

such as $r_1 = 0.05$ (Figure 3.3 (2)), there is almost no change from the equal case. This is due to the fact that $y(t)$ does not reach the homeostatic overload range for an extended period of time. However, when the $y(t)$ is in the homeostatic overload range, the negative effect it has on $M(t)$ is smaller. When r_2 is a large value such as $r_2 = 0.95$ (Figure 3.3 (3)), the negative effect that $y(t)$ being in the reactive homeostatic range has on $R(t)$ is increased, which pushes $y(t)$ into homeostatic overload for a longer period of time and potentially sooner in subsequent stress events, which further negatively impacts $M(t)$. When r_3 is set at a large value, such as $r_3 = 0.95$ (Figure 3.3 (4)), $R(t)$ recovers faster to the $M(t)$ level, but does not impact the amount of time $y(t)$ spends in homeostatic overload or the reactive homeostasis range. However, when r_3 takes on a small value, such as $r_3 = 0.05$ (Figure 3.3 (5)), $R(t)$ cannot recover as quickly to the $M(t)$ value, which causes the second stress event to push the mediator into homeostatic overload sooner and for a longer duration. In order to consider a small r_2 value such as $r_2 = 0.1$ and maintain the requirement $r_1 < r_2$, then r_1 must also adopt a smaller value such as $r_1 = 0.05$. In this case (Figure 3.3 (6)), the effect $y(t)$ being in homeostatic overload has on $M(t)$ and $R(t)$ is reduced, leading to a reduced time the mediator spends in homeostatic overload. If r_1 is set to a large value, such as $r_1 = 0.75$, and maintains the requirement $r_1 < r_2$, then r_2 must also adopt a large value, such as $r_2 = 0.95$. In this case (Figure 3.3 (7)), the effect that $y(t)$ being in homeostatic overload has on $M(t)$ and $R(t)$ is increased, which causes the mediator to spend more time homeostatic overload. When considering the six different combinations, four types proved to be particularly insightful scenarios: [1] a large r_2 is coupled with a large r_1 value, [2] a small r_3 , [3] a large r_3 , and [4] a small r_1 is coupled with a small r_2 .

In order to analyze how a connection between magnitude and duration might affect the mediator under different assumed functional relationships, we consider two stress events with the same magnitude in three different stress magnitude scenarios: $s_i = 0.2$ (Figures 3.4), $s_i = 0.4$ (Figures 3.5), and $s_i = 0.9$ (Figures 3.6). Within each of these scenarios, we consider duration as both a scalar of the magnitude and,

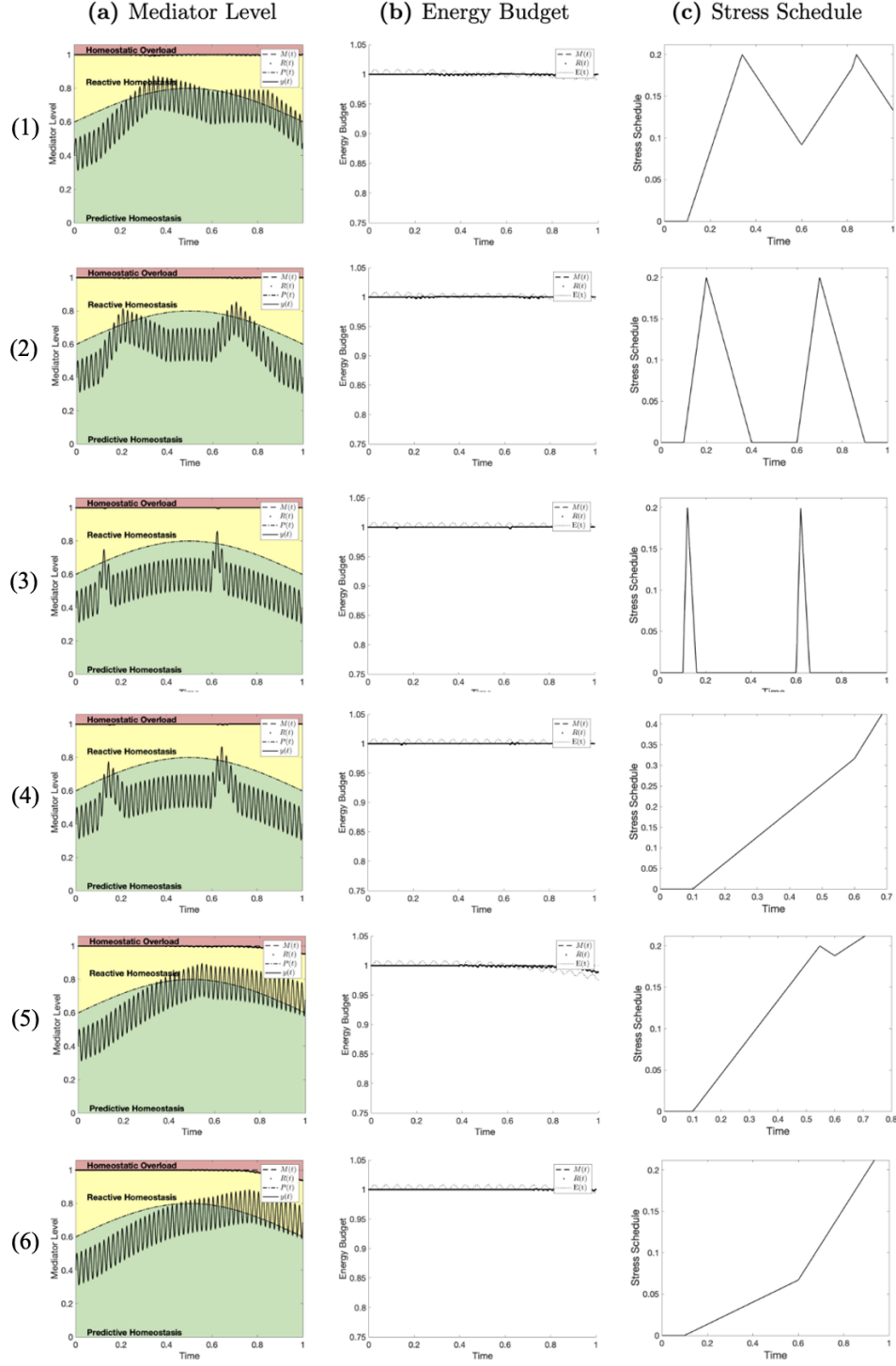


Figure 3.4: The magnitude (s_i) is 0.2 for both stress events. For (1)-(3), duration (σ_i) is a scalar function of the magnitude corresponding to $\sigma_i = 1.2s_i$ for (1), $\sigma_i = 0.5s_i$ for (2), and $\sigma_i = 0.1s_i$ for (3). For (4)-(6), (σ_i) is an exponential function of the magnitude corresponding to $\sigma_i = s_i^2$ for (4), $\sigma_i = s_i^{0.5}$ for (5), and $\sigma_i = s_i^{0.25}$ for (6).

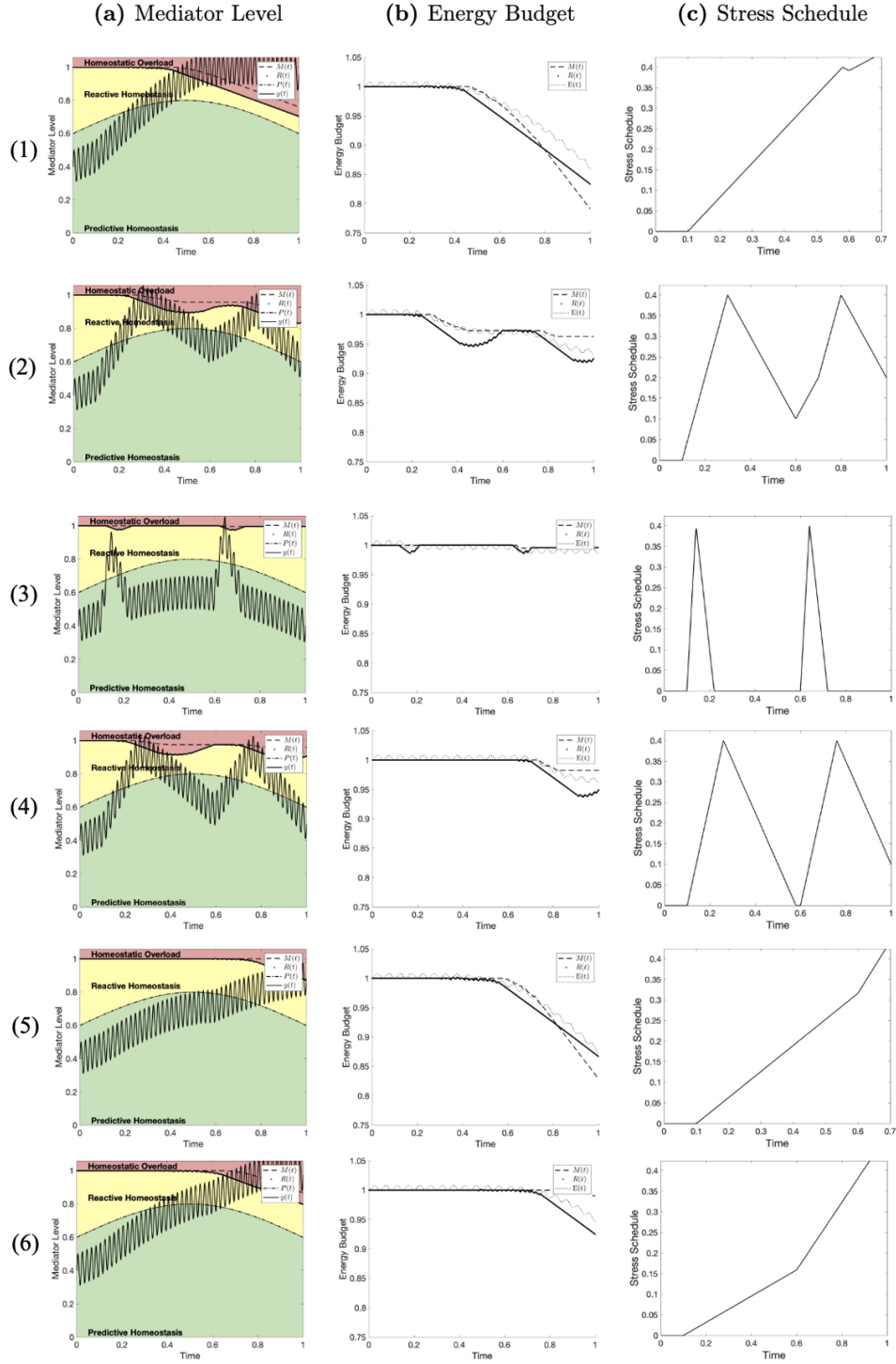


Figure 3.5: The magnitude (s_i) is 0.4 for both stress events. For (1)-(3), duration (σ_i) is a scalar function of the magnitude corresponding to $\sigma_i = 1.2s_i$ for (1), $\sigma_i = 0.5s_i$ for (2), and $\sigma_i = 0.1s_i$ for (3). For (4)-(6), (σ_i) is an exponential function of the magnitude corresponding to $\sigma_i = s_i^2$ for (4), $\sigma_i = s_i^{0.5}$ for (5), and $\sigma_i = s_i^{0.25}$ for (6).

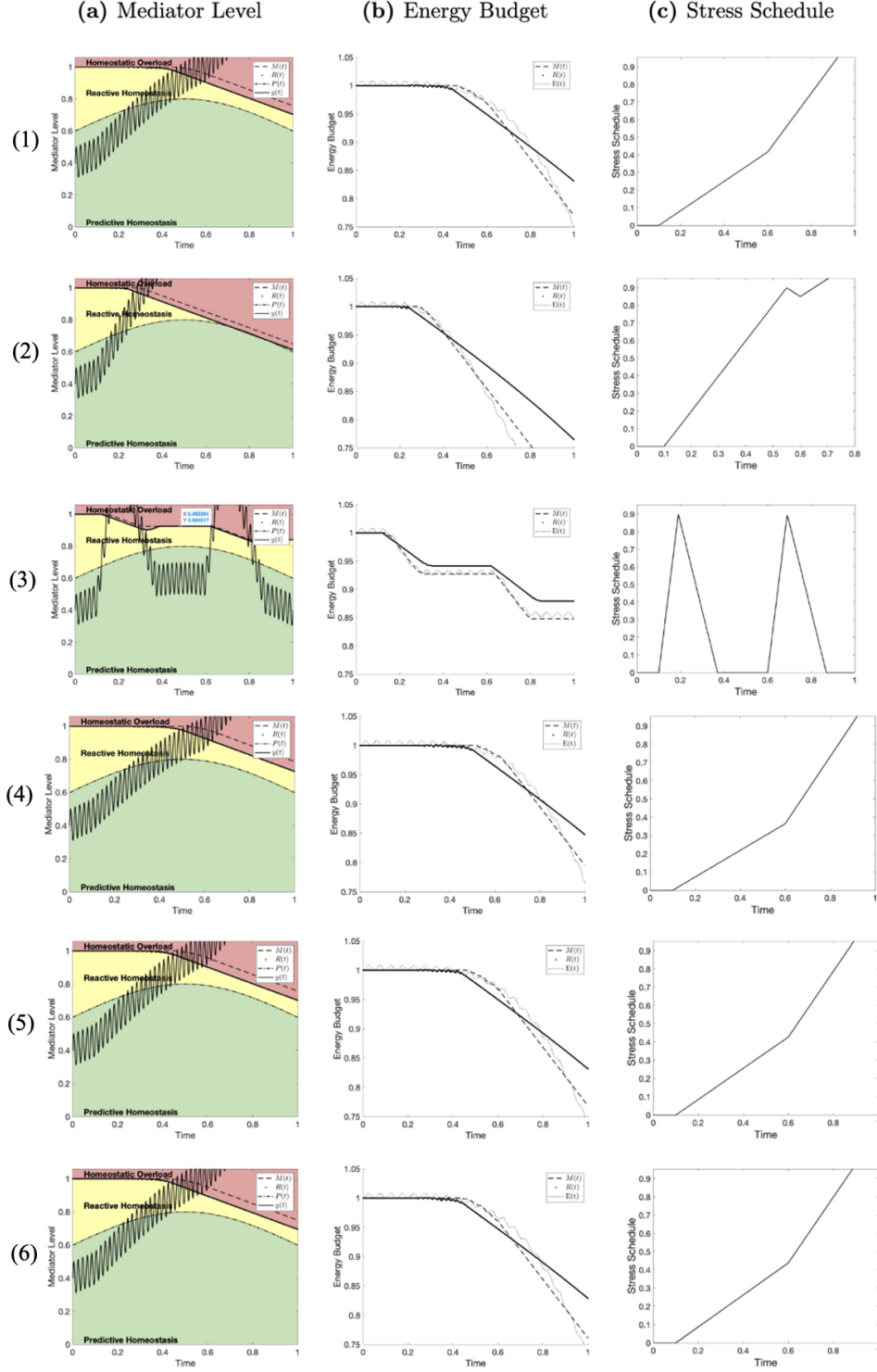


Figure 3.6: The magnitude (s_i) is 0.9 for both stress events. For (1)-(3), duration (σ_i) is a scalar function of the magnitude corresponding to $\sigma_i = 1.2s_i$ for (1), $\sigma_i = 0.5s_i$ for (2), and $\sigma_i = 0.1s_i$ for (3). For (4)-(6), (σ_i) is an exponential function of the magnitude corresponding to $\sigma_i = s_i^2$ for (4), $\sigma_i = s_i^{0.5}$ for (5), and $\sigma_i = s_i^{0.25}$ for (6).

separately, as an exponential of the magnitude with different assumed relationship-defining values. We contrast scale change functions of $\sigma_i = 0.1s_i$, $\sigma_i = 0.5s_i$, and $\sigma_i = 1.2s_i$ and exponential functions of $\sigma_i = s_i^2$, $\sigma_i = s_i^{0.5}$, and $\sigma_i = s_i^{0.25}$, and explore the effect the different combinations have on both the mediator and energy budget. We chose these values to provide a breadth of scenarios while maintaining biological plausibility and computational practicality.

When the duration is a scalar of magnitude, it has the largest effect of the mediator when the scale change is largest (Figures 3.4 (1), 3.5 (1), 3.6 (1)). The larger the scale change, the longer the animal spends in either reactive homeostasis or homeostatic overload, along with the second stress event potentially beginning before the first one has ended depending on the stress events' timing parameters. This means there is a loss of a stress-free period in which the animal could use as recovery. With the lower magnitude level (Figures 3.4 (1)-(3)), the mediator does not reach homeostatic overload, meaning the energy budget is not reduced. However, with higher magnitude levels (Figures 3.5 (1)-(3) and Figures 3.6 (1)-(3)), the energy budget can be greatly influenced. The higher magnitude increases the chance of the mediator experiencing homeostatic overload. Coupled with a duration of a high scalar (Figures 3.5 (1), 3.6 (1)), the mediator reaches homeostatic overload and is not able to recover, causing a rapid decrease in the energy budget. This is found with duration functions of $\sigma_i = 1.2s_i$ and $\sigma_i = 0.5s_i$. It is important to consider how the duration affects the peak magnitude timing. A shorter duration correlates with a sharper and earlier peak in the stress event schedule, which can cause the mediator to reach the reactive homeostasis and homeostatic overload ranges sooner and decrease $R(t)$ and $M(t)$. Assuming there is sufficient recovery to allow the mediator to leave homeostatic overload, this causes the mediator to re-enter homeostatic overload sooner with the second stress event. The earlier peak explains why a shorter duration can be more detrimental to the energy budget and the mediator than a more extended duration. Figures 3.6 (1)-(2), which have a magnitude value of $s_i = 0.9$ and duration functions of $\sigma_i = 1.2s_i$ and $\sigma_i = 0.5s_i$ show such an event occurring.

When duration is an exponential function of the magnitude, the biggest impact it has is changing the duration drastically enough that the second stress event starts before the first has finished, removing any stress-free period. An exponential function of $\sigma_i = s_i^2$ is the only function that allows the first stress event to resolve before the second starts. However, it only allows this when the magnitude level was 0.2 or 0.4 (Figures 3.4 (4) and 3.5 (4)). The other cases do not allow for any stress-free period and the mediator stays in homeostatic overload, causing a quick decline of the energy budget. It is important to consider that when the magnitude level is close to one, such as $s_i = 0.9$, then the exponential function duration is close to the magnitude level and the variance between different exponent values is less than when magnitude levels closer to zero. This is due to basic arithmetic: anything close to one, raised to an exponent, remains relatively close to one. Therefore, Figures 3.4(4)-(6) and Figures 3.5 (4)-3.5 (6) show more variance in exponential function scenarios than Figures 3.6(4)-3.6 (6).

3.7 Discussion

This paper expands on the work of [118], which presented the first quantitative model formulation of the reactive scope framework, by introducing an energy budget with consideration of multiple simultaneous mediators. We also explore the sensitivity of the model to parameter choices by two different types of analysis: [1] varying rate parameters to determine how they affect the system, and [2] how a connection between magnitude and duration affects the time spent in homeostatic overload.

The addition of an energy budget reveals aspects of stress events that affect the reduction of this budget. An energy budget can be used to as a reservoir for which an animal has to pull from to allocate energy to different functions or tasks. Stress events reduce the energy available for allocation to other functions. One example of such stress event is parental care [44]. Some of the basic parental functions needed for survival of offspring (*e.g.*, feeding, growth, and reproduction) require profound

energetic investments. Stress events then reduce the parent’s available energy, in turn affecting an individual’s fitness and the overall evolution of the species maturity and lifespan [68]. Here, we explore how the magnitude and duration of stress events are likely to impact an animal’s energy budget. There is a direct correlation between the magnitude and reduction in the energy budget, with a larger magnitude having a larger reduction. Similarly, there is a direct correlation between duration and reduction in the energy budget, with a long duration leading to an increased reduction. While these patterns are in no way surprising, our model provides a framework by which quantitative specification of the functional forms of these relationships can be translated into predictions about the health state outcomes for animals facing particular stressors over the course of their lives. Additionally, a stress event with a long duration can eliminate a recovery or rest period between stress events in which the animal has time to de-stress and the energy budget to stabilize.

Incorporating various mediators into the model allows for simultaneous comparison of the impact stress events have on different mediators, as well as consideration of how multiple mediators can concurrently reduce an energy budget. Each mediator has its own parameters that determine how a stress event is going to affect it. For example, in Figure 3.2(1), the first mediator reached homeostatic overload while the second mediator did not. This in turn, affects how each mediator reduces the energy budget.

In order to investigate how the stress parameters r_1 , r_2 , and r_3 impacts the thresholds $M(t)$ and $R(t)$ and further impacts the ranges a mediator level occupies, we consider six different combinations and compare them to the baseline in which $r_1 = r_2 = r_3$, as presented in [118]. We presented four significant types of scenarios. We would expect type[1] and type[2] scenarios to be relevant in studying physiological senescence, immunocompromise, or occupying a micronutrient deficient environment. Previous work has already shown that vitamins, minerals, and other micronutrients support a healthy immune system and without them, sickness is more likely and recovery compromised [91, 18, 1]. Additionally, age can affect the ability to recover,

as well as adequately manage stress [47, 111]. For example, age affects heart rate recovery after exercise through reduction of maximum heart rate values and cardiac output [111]. Together, these factors could explain large decline rates for thresholds $M(t)$ and $R(t)$, as well as a slow recovery of $R(t)$. In contrast to type[1] and type[2], type[3] and type[4] could be relevant in studying an animal occupying a micronutrient rich environment. This demonstrates how such environmental resource richness could translate directly into greater robustness and resilience to stress events, (*i.e.*, greater magnitudes or durations of stress events are required to send an animal into homeostatic overload and less time is required for the animal to recover when a stress event occurs) [111, 91, 18, 1].

Within the two functional forms involving magnitude and duration, there are four compelling combinations of events: [1] high magnitude with long duration, [2] high magnitude with short duration, [3] low magnitude with long duration, and [4] low magnitude with short duration.

Combination[1] corresponds to when the magnitude is 0.9 ($s_i=0.9$) and the duration is either $\sigma_i = 1.2s_i$ (3.6 (1)) or $\sigma_i = 0.25$ (3.6 (6)). Both lead to the mediator reaching homeostatic overload and threshold functions declining steadily. Biologically, this could represent a stress event such as childcare, in which rearing offspring makes demands on an animal physically and mentally until the offspring is self-sufficient. Additional factors such as father absence or mental conditions lead to increased stress on the parent(s) [117, 93].

Combination[2] could represent an occurrence such as being chased by a predator. Studies have shown that being chased by a predator or fast moving object can result in elevated corticosterone levels and elicit defensive responses [98, 66]. Further, increased predation stress events over a period of time can cause additional negative affects such as reproductive changes, reduced overall fitness, and overall population declines [8]. A stress occurrence like being chased by a predator can be represented in Figures 3.6 (3)-(4) when the magnitude is 0.9 ($s_i = 0.9$) and the duration is either $\sigma_i = 0.1s_i$ or $\sigma_i = s_i^2$.

Combination[3] can represent instants such as habitat degradation. One study on Northern saw-whet owls compares stress levels of birds in fragmented versus non-fragmented habitats, conveying how habitat degradation can cause changes in movement patterns, food availability, and cross-species interactions [52]. Here, the effects of this can be represented when the magnitude is 0.2 ($s_i = 0.2$) and the duration is either $\sigma_i = 1.2s_i$ (Figure 3.4 (1)) or $\sigma_i = s_i^{0.25}$ (Figure 3.4 (6)).

Combination[4] is when the magnitude is $s_i = 0.2$ and duration either $\sigma_i = 0.1s_i$ or $\sigma_i = s_i^2$, which is shown in Figures 3.4 (3) and 3.4 (4), reflecting an occurrence such as delayed feeding times. This is consistent with empirical evidence, for example, a study of captive primates showed changes in behavior and activity levels around feeding times and an increase in stress related behaviors when feeding is delayed [116].

Across these scenarios, it can be seen that the less detrimental case is when magnitude is low and duration is short, which is consistent with logical physiological behavior. Additionally, based on biological scenario specific parameters, predictions for the speed in which an animal reaches the reactive homeostatic and homeostatic overload ranges along with the time spent there can be made.

Higher magnitudes causes the $y(t)$ function to continue on its upward slope for an extended period of time, causing the mediator to enter into or go further in the reactive homeostasis and homeostatic overload ranges and delaying the time they exit or remove it completely. Once magnitudes reach a sufficiently high value, homeostatic overload and negative health effects is unavoidable. When coupled with a long duration, a high magnitude can remove the ability for the mediator to recover or exit homeostatic overload. Shorter durations lead to an increased slope of the $y(t)$ function, causing the mediator to reach the reactive homeostasis and homeostatic overload ranges sooner, but also exit them at a faster rate, if the parameters allow an exit. The increased slope associated with a shorter duration can be more detrimental than a long duration with a high magnitude (Figure 3.6 (2)). This comparatively shorter duration causes peak magnitude to occur sooner, pushing the mediator into homeostatic overload sooner. However, the magnitude is high enough for the mediator

to increase for a long enough time to not allow the mediator to leave homeostatic overload for a recovery period before the next stress event, ultimately leading to spending more time in homeostatic overload.

Overall, these scenarios can predict health states and outcomes over time given a pattern of magnitudes and durations of stress events experienced over an animal's lifetime. Actions such as extending the duration or efforts to reduce the magnitude can help the animal by reducing time in homeostatic overload or allowing a recovery period between stress events.

3.8 Limitations and Future Directions

There are several further additions that could improve the current energy budget model. First, each mediator currently has the same effect on the energy budget based on how far the mediator is into the reactive homeostasis and homeostatic overload ranges. However, this should change based on the biology of the subject and the studied mediators since, for example, behavioral changes might have less of an impact on the energy budget than an immune response. Environmental stressors such as cold temperatures can induce behavior changes such as increased food intake [124]. However, if abundant food intake is an option, then the energy budget should not be depleted in the same way as if there were inadequate food resources. Immune responses can drain energy levels through physiological responses such as increased oxygen consumption, which can be the case in response to a fever [33]. The physiological condition and challenge scenario in which the animal is experiencing stressors should be considered in choosing the mediators' parameters. Some questions surrounding the energy budget are: How is this energy budget built? Does it rely exclusively on caloric intake? Are there certain mediators that should not be considered as independent contributing factors (i.e., are two or more mediators acting in sufficient conjunction that they constitute only a single combined depletion of the energy budget)? The literature provides different strategies for formulating an

energy budget, such as foundations in thermodynamics or bioenergetics with species specific parameters such as metabolic and environmental [65, 58]. This means making an appropriate choice for the method used to formulate the energy budget, and how mediators affect it, is critical to the utility of the model. Additionally, the acclimation to stress an animal could develop over time could be included in the model. Acting in a contrary direction to the build up of ‘wear and tear’, repeated stress could build resilience and allow increased longevity [73].

3.9 Conclusion

[118] presented the first quantitative framework capturing the reactive scope model as conceptualized by [99] in which mediators could occupy different states including predictive homeostasis, reactive homeostasis, and homeostatic overload. That work demonstrated how extended time in the reactive homeostasis state could cause degradation and eventually lead to homeostatic overload, which further leads to detrimental effects on the animal. Here, we add an energy budget and consider how multiple mediators may affect an individual’s energy reservoir. A more intense stress event, or higher magnitude, causes a larger decrease in the energy budget (Figure 3.2 (2)) by expanding the time the mediator function is increasing. Additionally, a shorter duration correlates with a higher first derivative of the $y(t)$ function, or steeper slope of the mediator function. This causes the mediator to reach reactive homeostasis or homeostatic overload sooner, potentially increasing the time spent in those states and degrading the energy budget. Duration impacts or eliminates the time for recovery between stressors (Figure 3.2 (3)).

Considering multiple mediators allows for the analysis of the potential compounding effects among mediators. Empirical investigation is still needed to identify the different, independent and synergistic impacts of each mediator on the overall energy budget. However, this creates a more holistic view of how a stress event is likely to affect the animal.

Parameter analysis demonstrates how the rate parameters drive the decrease and recovery of thresholds, potentially making it easier for an animal to reach homeostatic overload, such as when the recovery rate for $R(t)$ is small (Figure 3.3 (5)). This lowers the threshold for reaching homeostatic overload, where the mediator reaches the detrimental state at a lower level and possibly sooner than with a high recovery rate. Coupling magnitude and duration allows us to consider such questions as how a moderate or short duration stress event can be more detrimental than a long duration because the peak magnitude occurs sooner, causing the mediator to spend more time in homeostatic overload (Figures 3.6 (1)-(2)). The downward slope of threshold curves of the characteristic ranges represent the ‘wear and tear’ the mediator experiences. The longer a mediator spends in either reactive homeostasis or homeostatic overload, the more degradation of the threshold curves occur, which could make subsequent stressors send the mediator into detrimental ranges sooner and for longer. Over time, repeated stress events could cause enough ‘wear and tear’ to lower the threshold curves to such critically low levels that the mediator experiences homeostatic overload enough to cause significant health repercussions or an early demise.

Overall, the addition of an energy budget, along with multiple mediators, provides a more complete picture of how stress affects an animal. Coupled with parameter analysis, this increases the power of the quantitative model to aid in making accurate, life-history-tailored predictions about the impacts of stress events and the temporal dynamics of reactive scope and health outcomes over an animal’s life.

Bibliography

- [1] Mary Adjepong, Pius Agbenorku, Patricia Brown, and Ibok Oduro. The role of antioxidant micronutrients in the rate of recovery of burn patients: a systematic review. *Burns & trauma*, 4, 2016. [125](#), [126](#)
- [2] GLENN D Aguilar. Philippine fishing boats. *DA-BFAR (Department of Agriculture-Bureau of Fisheries and Aquatic Resources)*. In *Turbulent seas: The Status of Philippine Marine Fisheries, Coastal Resource Management Project of Department of Environment and Natural Resources, Cebu City, Philippines*. 378p, pages 118–121, 2004. [79](#)
- [3] Muhammad A Ahmad and Ankur Teredesai. Modeling spread of ideas in online social networks. In *Proceedings of the fifth Australasian conference on Data mining and analytics-Volume 61*, pages 185–190, 2006. [4](#)
- [4] Barbara L Andersen, Janice K Kiecolt-Glaser, and Ronald Glaser. A biobehavioral model of cancer stress and disease course. *American psychologist*, 49(5):389, 1994. [4](#)
- [5] Marissa L Baskett, Roger M Nisbet, Carrie V Kappel, Peter J Mumby, and Steven D Gaines. Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. *Global Change Biology*, 16(4):1229–1246, 2010. [50](#)
- [6] Christophe Béné, Luc Doyen, and Daniel Gabay. A viability analysis for a bio-economic model. *Ecological economics*, 36(3):385–396, 2001. [4](#)

- [7] G Bertram Jr et al. *Population dynamics: alternative models*. Elsevier, 2013. [5](#)
- [8] Rudy Boonstra, David Hik, Grant R Singleton, and Alexander Tinnikov. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological monographs*, 68(3):371–394, 1998. [126](#)
- [9] Emile Borel. The theory of play and integral equations with skew symmetric kernels. *Econometrica: journal of the Econometric Society*, pages 97–100, 1953. [53](#)
- [10] W Thomas Boyce and Bruce J Ellis. Biological sensitivity to context: I. an evolutionary–developmental theory of the origins and functions of stress reactivity. *Development and psychopathology*, 17(2):271–301, 2005. [109](#)
- [11] Laura A Brannelly, Hamish I McCallum, Laura F Grogan, Cheryl J Briggs, Maria P Ribas, Matthijs Hollanders, Thais Sasso, Mariel Familiar López, David A Newell, and Auston M Kilpatrick. Mechanisms underlying host persistence following amphibian disease emergence determine appropriate management strategies. *Ecology letters*, 24(1):130–148, 2021. [20](#)
- [12] Fred Brauer, Carlos Castillo-Chavez, Zhilan Feng, et al. *Mathematical models in epidemiology*, volume 32. Springer, 2019. [5](#)
- [13] Creagh W Breuner, John C Wingfield, and L Michael Romero. Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, gambel’s white-crowned sparrow. *Journal of Experimental Zoology*, 284(3):334–342, 1999. [109](#)
- [14] Carol Brewer. Outreach and partnership programs for conservation education where endangered species conservation and research occur. *Conservation Biology*, 16(1):4–6, 2002. [51](#)

- [15] Erwin H Bulte and G Cornelis van Kooten. Harvesting and conserving a species when numbers are low: population viability and gambler’s ruin in bioeconomic models. *Ecological Economics*, 37(1):87–100, 2001. [4](#)
- [16] Colin F Camerer. Progress in behavioral game theory. *Journal of economic perspectives*, 11(4):167–188, 1997. [51](#)
- [17] Sanya Carley, Tom P Evans, and David M Konisky. Adaptation, culture, and the energy transition in american coal country. *Energy Research & Social Science*, 37:133–139, 2018. [6](#), [26](#)
- [18] Michael P Casaer and Rinaldo Bellomo. Micronutrient deficiency in critical illness: an invisible foe? *Intensive Care Medicine*, 45(8):1136–1139, 2019. [125](#), [126](#)
- [19] Hal Caswell. Matrix methods for population analysis. In *Structured-population models in marine, terrestrial, and freshwater systems*, pages 19–58. Springer, 1997. [12](#)
- [20] Admire Chanyandura, Victor K Muposhi, Edson Gandiwa, and Never Muboko. An analysis of threats, strategies, and opportunities for african rhinoceros conservation. *Ecology and Evolution*, 11(11):5892–5910, 2021. [80](#)
- [21] Raj Chovatiya and Ruslan Medzhitov. Stress, inflammation, and defense of homeostasis. *Molecular cell*, 54(2):281–288, 2014. [108](#)
- [22] Colin W Clark. The economics of overexploitation: Severe depletion of renewable resources may result from high discount rates used by private exploiters. *Science*, 181(4100):630–634, 1973. [4](#)
- [23] Colin W Clark. Profit maximization and the extinction of animal species. *Journal of Political Economy*, 81(4):950–961, 1973. [4](#)

- [24] Colin W Clark. *Mathematical bioeconomics: the mathematics of conservation*, volume 91. John Wiley & Sons, 2010. [3](#)
- [25] Colin W Clark and R Lamberson. An economic history and analysis of pelagic whaling. *Marine policy*, 6(2):103–120, 1982. [4](#)
- [26] Shelley Clarke, Eleanor J Milner-Gulland, and Trond Bjørndal. Social, economic, and regulatory drivers of the shark fin trade. *Marine Resource Economics*, 22(3):305–327, 2007. [50](#)
- [27] Steven Edward Cohrun. Understanding and enhancing neighborhood sense of community. *Journal of planning literature*, 9(1):92–99, 1994. [24](#)
- [28] Andrew Collins and Patrick T Hester. Colonel blotto games and lancaster’s equations: A novel military modeling combination. 2012. [52](#)
- [29] Jon M Conrad. Open access and extinction of the passenger pigeon in north america. *Natural Resource Modeling*, 18(4):501–519, 2005. [4](#)
- [30] Enric Cortés. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation biology*, 16(4):1048–1062, 2002. [50](#)
- [31] Scott Crosson. Anticipating exit from north carolina’s commercial fisheries. *Society & Natural Resources*, 28(7):797–806, 2015. [25](#)
- [32] Andrea Dell’Apa, M Chad Smith, and Mahealani Y Kaneshiro-Pineiro. The influence of culture on the international management of shark finning. *Environmental management*, 54:151–161, 2014. [50](#), [63](#)
- [33] Gregory E Demas. The energetics of immunity: a neuroendocrine link between energy balance and immune function. *Hormones and Behavior*, 45(3):173–180, 2004. [128](#)

- [34] Martin Drechsler, Frank Wätzold, Karin Johst, Holger Bergmann, and Josef Settele. A model-based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. *Biological conservation*, 140(1-2):174–186, 2007. [50](#)
- [35] SE DuRant, ML Arciniega, CM Bauer, and LM Romero. A test of reactive scope: Reducing reactive scope causes delayed wound healing. *General and Comparative Endocrinology*, 236:115–120, 2016. [109](#), [110](#)
- [36] Phoebe D Edwards, Skyler J Mooney, Curtis O Bosson, Ilapreet Toor, Rupert Palme, Melissa M Holmes, and Rudy Boonstra. The stress of being alone: removal from the colony, but not social subordination, increases fecal cortisol metabolite levels in eusocial naked mole-rats. *Hormones and behavior*, 121:104720, 2020. [109](#)
- [37] WK Estes. Mathematical models in psychology. *A Handbook for Data Analysis in the Behavioral Sciences: Volume 1: Methodological Issues Volume 2: Statistical Issues*, page 3, 2014. [110](#)
- [38] KT Everatt, R Kokes, and C Lopez Pereira. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, 28(14):4099–4114, 2019. [49](#)
- [39] Michael Fabinyi. Historical, cultural and social perspectives on luxury seafood consumption in china. *Environmental Conservation*, 39(1):83–92, 2012. [51](#)
- [40] Scott Farrow. Extinction and market forces: two case studies. *Ecological Economics*, 13(2):115–123, 1995. [4](#)
- [41] Francesco Ferretti, David MP Jacoby, Mariah O Pfleger, Timothy D White, Felix Dent, Fiorenza Micheli, Andrew A Rosenberg, Larry B Crowder, and Barbara A Block. Shark fin trade bans and sustainable shark fisheries. *Conservation Letters*, 13(3):e12708, 2020. [51](#)

- [42] Andrés García, Gerardo Ceballos, and Ricardo Adaya. Intensive beach management as an improved sea turtle conservation strategy in Mexico. *Biological Conservation*, 111(2):253–261, 2003. [79](#)
- [43] David Gavaghan, Alan Garny, Philip K Maini, and Peter Kohl. Mathematical models in physiology. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 364(1842):1099–1106, 2006. [110](#)
- [44] David L Goldstein. Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *American Zoologist*, 28(3):829–844, 1988. [124](#)
- [45] Sanghai Guan, Jingjing Wang, Haipeng Yao, Chunxiao Jiang, Zhu Han, and Yong Ren. Colonel blotto games in network systems: Models, strategies, and applications. *IEEE Transactions on Network Science and Engineering*, 7(2):637–649, 2019. [52](#)
- [46] Flávia Maria Guebert, Mário Barletta, and Monica Ferreira da Costa. Threats to sea turtle populations in the western Atlantic: poaching and mortality in small-scale fishery gears. *Journal of Coastal Research*, (65):42–47, 2013. [49](#)
- [47] Marcia C Haigis and Bruce A Yankner. The aging stress response. *Molecular cell*, 40(2):333–344, 2010. [126](#)
- [48] Lee Hannah, Guy F Midgley, and D Millar. Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, 11(6):485–495, 2002. [50](#)
- [49] Fengzhi He, Christiane Zarfl, Vanessa Bremerich, Alex Henshaw, William Darwall, Klement Tockner, and Sonja C Jaehrig. Disappearing giants: a review of threats to freshwater megafauna. *Wiley Interdisciplinary Reviews: Water*, 4(3):e1208, 2017. [50](#)

- [50] Friedo Herbig and Anthony Minnaar. Pachyderm poaching in africa: Interpreting emerging trends and transitions. *Crime, Law and Social Change*, 71:67–82, 2019. [80](#)
- [51] Damián G Hernández and Damián H Zanette. Evolutionary dynamics of resource allocation in the colonel blotto game. *Journal of Statistical Physics*, 151:623–636, 2013. [52](#)
- [52] Heather Lynn Hinam and Colleen Cassady St Clair. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of northern saw-whet owls. *Biological Conservation*, 141(2):524–535, 2008. [127](#)
- [53] Frederic L Holmes. Claude bernard, the” milieu intérieur”, and regulatory physiology. *History and Philosophy of the Life Sciences*, pages 3–25, 1986. [108](#)
- [54] Evan M Howard, Justin L Penn, Hartmut Frenzel, Brad A Seibel, Daniele Bianchi, Lionel Renault, Fayçal Kessouri, Martha A Sutula, James C McWilliams, and Curtis Deutsch. Climate-driven aerobic habitat loss in the california current system. *Science advances*, 6(20):eaay3188, 2020. [20](#)
- [55] Jeffrey A Hutchings and John D Reynolds. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience*, 54(4):297–309, 2004. [6](#)
- [56] David MP Jacoby, Francesco Ferretti, Robin Freeman, Aaron B Carlisle, Taylor K Chapple, David J Curnick, Jonathan J Dale, Robert J Schallert, David Tickler, and Barbara A Block. Shark movement strategies influence poaching risk and can guide enforcement decisions in a large, remote marine protected area. *Journal of Applied Ecology*, 57(9):1782–1792, 2020. [50](#)

- [57] Subit K Jain, Swati Tyagi, Neeraj Dhiman, and Jehad Alzabut. Study of dynamic behaviour of psychological stress during covid-19 in india: A mathematical approach. *Results in Physics*, 29:104661, 2021. [3](#)
- [58] Marko Jusup, Tânia Sousa, Tiago Domingos, Velimir Labinac, Nina Marn, Zhen Wang, and Tin Klanjšček. Physics of metabolic organization. *Physics of life reviews*, 20:1–39, 2017. [129](#)
- [59] TK Kar and H Matsuda. A bioeconomic model of a single-species fishery with a marine reserve. *Journal of environmental management*, 86(1):171–180, 2008. [4](#)
- [60] Jahangir Karimi and Zhiping Walter. Corporate entrepreneurship, disruptive business model innovation adoption, and its performance: The case of the newspaper industry. *Long range planning*, 49(3):342–360, 2016. [26](#)
- [61] Daniel Katzman, Jessica Moreno, Jason Noelanders, and Mark Winston-Galant. 10.4: Using eigenvalues and eigenvectors to find stability and solve odes. *Engineering LibreTexts*. [12](#)
- [62] Muhammad Zahoor Khan and Muhammad Zahoor. An overview of brucellosis in cattle and humans, and its serological and molecular diagnosis in control strategies. *Tropical medicine and infectious disease*, 3(2):65, 2018. [7](#)
- [63] Pushmeet Kohli, Michael Kearns, Yoram Bachrach, Ralf Herbrich, David Stillwell, and Thore Graepel. Colonel blotto on facebook: The effect of social relations on strategic interaction. In *Proceedings of the 4th Annual ACM Web Science Conference*, pages 141–150, 2012. [52](#)
- [64] Timothy Kuiper, Blessing Kavhu, Nobesuthu A Ngwenya, Roseline Mandisodza-Chikerema, and EJ Milner-Gulland. Rangers and modellers collaborate to build and evaluate spatial models of african elephant poaching. *Biological Conservation*, 243:108486, 2020. [50](#)

- [65] Romain Lavaud, Ramón Filgueira, and Starrlight Augustine. The role of dynamic energy budgets in conservation physiology. *Conservation Physiology*, 9(1):coab083, 2021. [129](#)
- [66] Ji-Hye Lee, Sunwhi Kimm, Jung-Soo Han, and June-Seek Choi. Chasing as a model of psychogenic stress: characterization of physiological and behavioral responses. *Stress*, 21(4):323–332, 2018. [126](#)
- [67] Craig Leisher, Sangeeta Mangubhai, Sebastiaan Hess, Hesti Widodo, Tri Soekirman, Salomina Tjoe, Stevanus Wawiyai, S Neil Larsen, Lukas Rumetna, A Halim, et al. Measuring the benefits and costs of community education and outreach in marine protected areas. *Marine Policy*, 36(5):1005–1011, 2012. [78](#)
- [68] Konstadia Lika and Sebastiaan ALM Kooijman. Life history implications of allocation to growth versus reproduction in dynamic energy budgets. *Bulletin of Mathematical Biology*, 65(5):809–834, 2003. [125](#)
- [69] Matthew Linkie, Deborah J Martyr, Jeremy Holden, Achmad Yanuar, Alip T Hartana, Jito Sugardjito, and Nigel Leader-Williams. Habitat destruction and poaching threaten the sumatran tiger in kerinci seblat national park, sumatra. *Oryx*, 37(1):41–48, 2003. [49](#)
- [70] Siyu Lu, Fang Wei, and Guolin Li. The evolution of the concept of stress and the framework of the stress system. *Cell Stress*, 5(6):76, 2021. [109](#)
- [71] Jane M Macharia, Thuita Thenya, and George G Ndiritu. Management of highland wetlands in central kenya: The importance of community education, awareness and eco-tourism in biodiversity conservation. *Biodiversity*, 11(1-2):85–90, 2010. [51](#)
- [72] Aditya Mahajan and Demosthenis Teneketzis. Multi-armed bandit problems. In *Foundations and applications of sensor management*, pages 121–151. Springer, 2008. [53](#)

- [73] Valeria Marasco, Winnie Boner, Britt Heidinger, Kate Griffiths, and Pat Monaghan. Repeated exposure to stressful conditions can have beneficial effects on survival. *Experimental gerontology*, 69:170–175, 2015. [129](#)
- [74] VM Marsh, W Mutemi, ES Some, A Haaland, and RW Snow. Evaluating the community education programme of an insecticide-treated bed net trial on the kenyan coast. *Health policy and planning*, 11(3):280–291, 1996. [79](#)
- [75] Joyce Maschinski, Samuel J Wright, and Caroline Lewis. The critical role of the public: plant conservation through volunteer and community outreach projects. *Plant reintroduction in a changing climate: Promises and perils*, pages 53–69, 2012. [51](#)
- [76] Bruce S McEwen and John C Wingfield. The concept of allostasis in biology and biomedicine. *Hormones and behavior*, 43(1):2–15, 2003. [110](#)
- [77] Margaret A McKean. Common property: what is it, what is it good for, and what makes it work. *People and forests: Communities, institutions, and governance*, pages 27–55, 2000. [8](#)
- [78] Susan Michie. Causes and management of stress at work. *Occupational and environmental medicine*, 59(1):67–72, 2002. [21](#)
- [79] Manfred Milinski and Claus Wedekind. Working memory constrains human cooperation in the prisoner’s dilemma. *Proceedings of the National Academy of Sciences*, 95(23):13755–13758, 1998. [61](#)
- [80] Byungjoon Min and Maxi San Miguel. Competing contagion processes: Complex contagion triggered by simple contagion. *Scientific reports*, 8(1):10422, 2018. [5](#), [6](#)
- [81] Jenny Moreno, Alejandro Lara, and Mauricio Torres. Community resilience in response to the 2010 tsunami in chile: The survival of a small-scale fishing

- community. *International Journal of Disaster Risk Reduction*, 33:376–384, 2019. [3](#), [5](#)
- [82] Erich Möstl and Rupert Palme. Hormones as indicators of stress. *Domestic animal endocrinology*, 23(1-2):67–74, 2002. [109](#)
- [83] Robin Naidoo and Taylor H Ricketts. Mapping the economic costs and benefits of conservation. *PLoS biology*, 4(11):e360, 2006. [21](#)
- [84] Matthias Nemeth, Elisabeth Pschernig, Bernard Wallner, and Eva Millesi. Non-invasive cortisol measurements as indicators of physiological stress responses in guinea pigs. *PeerJ*, 4:e1590, 2016. [109](#)
- [85] Vincent Nijman. Illegal trade in protected sharks: The case of artisanal whale shark meat fisheries in java, indonesia. *Animals*, 13(16):2656, 2023. [63](#)
- [86] RM Nisbet, EB Muller, K Lika, and SALM Kooijman. From molecules to ecosystems through dynamic energy budget models. *Journal of animal ecology*, pages 913–926, 2000. [110](#)
- [87] KEN Norris. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology*, 41(3):413–426, 2004. [50](#)
- [88] G Oviedo. Community conserved areas in south america. *parks* 16 (1): 49–55, 2006. [63](#)
- [89] Norman Owen-Smith. *Introduction to modeling in wildlife and resource conservation*. John Wiley & Sons, 2009. [5](#)
- [90] D Pal, GS Mahaptra, and GP Samanta. Optimal harvesting of prey–predator system with interval biological parameters: a bioeconomic model. *Mathematical biosciences*, 241(2):181–187, 2013. [4](#)

- [91] Francesco Pecora, Federica Persico, Alberto Argentiero, Cosimo Neglia, and Susanna Esposito. The role of micronutrients in support of the immune response against viral infections. *Nutrients*, 12(10):3198, 2020. [125](#), [126](#)
- [92] Robert S Pindyck. Uncertainty in the theory of renewable resource markets. *The Review of Economic Studies*, 51(2):289–303, 1984. [4](#)
- [93] Ewa Pisula and Anna Porebowicz-Dörsmann. Family functioning, parenting stress and quality of life in mothers and fathers of polish children with high functioning autism or asperger syndrome. *PloS one*, 12(10):e0186536, 2017. [126](#)
- [94] Jessica Pykett, Tess Osborne, and Bernd Resch. From urban stress to neurourbanism: how should we research city well-being? *Annals of the American Association of Geographers*, 110(6):1936–1951, 2020. [4](#)
- [95] John M Raeburn. Toward a sense of community: Comprehensive community projects and community houses. *Journal of Community Psychology*, 14(4):391–398, 1986. [25](#)
- [96] Tharmalingam Ramesh, Riddhika Kalle, Havard Rosenlund, and Colleen T Downs. Low leopard populations in protected areas of maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecology and evolution*, 7(6):1964–1973, 2017. [50](#)
- [97] Brian Roberson. The colonel blotto game. *Economic Theory*, 29(1):1–24, 2006. [53](#)
- [98] Thomas Rödl, Silke Berger, L Michael Romero, and Martin Wikelski. Tameness and stress physiology in a predator-naive island species confronted with novel predation threat. *Proceedings of the Royal Society B: Biological Sciences*, 274(1609):577–582, 2007. [126](#)

- [99] L Michael Romero, Molly J Dickens, and Nicole E Cyr. The reactive scope model—a new model integrating homeostasis, allostasis, and stress. *Hormones and behavior*, 55(3):375–389, 2009. [xxiv](#), [108](#), [110](#), [111](#), [129](#)
- [100] Alexander K Saeri, Tegan Cruwys, Fiona Kate Barlow, Samantha Stronge, and Chris G Sibley. Social connectedness improves public mental health: Investigating bidirectional relationships in the new zealand attitudes and values survey. *Australian & New Zealand Journal of Psychiatry*, 52(4):365–374, 2018. [5](#), [24](#)
- [101] Darby E Saxbe, Lane Beckes, Sarah A Stoycos, and James A Coan. Social allostasis and social allostatic load: A new model for research in social dynamics, stress, and health. *Perspectives on Psychological Science*, 15(2):469–482, 2020. [109](#)
- [102] Galina Schwartz, Patrick Loiseau, and Shankar S Sastry. The heterogeneous colonel blotto game. In *2014 7th international conference on NETwork Games, COntrol and OPTimization (NetGCoop)*, pages 232–238. IEEE, 2014. [52](#)
- [103] DS Shiffman and RE Hueter. A united states shark fin ban would undermine sustainable shark fisheries. *Marine Policy*, 85:138–140, 2017. [51](#)
- [104] Xin Shuai, Shanshan Chen, Ying Ding, Yuyin Sun, Jerome Busemeyer, and Jie Tang. There is more than complex contagion: An indirect influence analysis on twitter. In *Proceedings of the ACM SIGKDD Workshop on Mining Data Semantics*, MDS ’12, New York, NY, USA, 2012. Association for Computing Machinery. [6](#)
- [105] Karl Sigmund. Introduction to evolutionary game theory. *Evolutionary game dynamics*, 69:1–26, 2011. [54](#)
- [106] Karl Sigmund and Martin A Nowak. Evolutionary game theory. *Current Biology*, 9(14):R503–R505, 1999. [54](#)

- [107] Andrea Šimková, Jiří Jarkovský, Božena Koubková, Vlastimil Baruš, and Miroslav Prokeš. Associations between fish reproductive cycle and the dynamics of metazoan parasite infection. *Parasitology Research*, 95:65–72, 2005. [7](#)
- [108] Simon Stephens, Christopher McLaughlin, and Katrina McLaughlin. Small business in a time of crisis: A five stage model of business grief. *Journal of Business Venturing Insights*, 16:e00282, 2021. [2](#)
- [109] Peter Sterling. Allostasis: a new paradigm to explain arousal pathology. *Handbook of life stress, cognition and health*, 1988. [110](#)
- [110] R Sukumar, Uma Ramakrishnan, and JA Santosh. Impact of poaching on an asian elephant population in periyar, southern india: a model of demography and tusk harvest. In *Animal Conservation forum*, volume 1, pages 281–291. Cambridge University Press, 1998. [50](#)
- [111] Jelena Suzic Lazic, Milica Dekleva, Ivan Soldatovic, Roman Leischik, Slavica Suzic, Dragan Radovanovic, Biljana Djuric, Dejan Nesic, Milivoje Lazic, and Sanja Mazic. Heart rate recovery in elite athletes: the impact of age and exercise capacity. *Clinical physiology and functional imaging*, 37(2):117–123, 2017. [126](#)
- [112] Yuki Takayanagi and Tatsushi Onaka. Roles of oxytocin in stress responses, allostasis and resilience. *International journal of molecular sciences*, 23(1):150, 2021. [109](#)
- [113] M Scott Taylor. Buffalo hunt: International trade and the virtual extinction of the north american bison. *American Economic Review*, 101(7):3162–3195, 2011. [4](#)
- [114] V Dao Truong, Nam VH Dang, and C Michael Hall. The marketplace management of illegal elixirs: illicit consumption of rhino horn. *Consumption Markets & Culture*, 19(4):353–369, 2016. [50](#)

- [115] C Mirjam Van Praag. Business survival and success of young small business owners. *Small business economics*, 21:1–17, 2003. [2](#)
- [116] Corri Waitt and Hannah M Buchanan-Smith. What time is feeding?: How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. *Applied animal behaviour science*, 75(1):75–85, 2001. [127](#)
- [117] Marsha Weinraub and Barbara M Wolf. Effects of stress and social supports on mother-child interactions in single-and two-parent families. *Child development*, pages 1297–1311, 1983. [126](#)
- [118] Justin Wright, Kelly Buch, Ursula K Beattie, Brenna MG Gormally, L Michael Romero, and Nina Fefferman. A mathematical representation of the reactive scope model. *Journal of Mathematical Biology*, 87(3):51, 2023. [xxiv](#), [xxv](#), [108](#), [109](#), [110](#), [111](#), [112](#), [113](#), [115](#), [116](#), [117](#), [124](#), [125](#), [129](#)
- [119] Yongle Wu, Beibei Wang, and KJ Ray Liu. Optimal power allocation strategy against jamming attacks using the colonel blotto game. In *GLOBECOM 2009-2009 IEEE Global Telecommunications Conference*, pages 1–5. IEEE, 2009. [52](#)
- [120] Bo Xia, Zhichao Ma, and Yingyue Hu. Research on the relationship between physical exercise, psychological flexibility and positive emotion of college students based on computer mathematical model. In *Journal of Physics: Conference Series*, volume 1578, page 012009. IOP Publishing, 2020. [3](#)
- [121] Chao Yan, Jinlong Xiao, Di Chen, Simon P Turner, Zhiwei Li, Hao Liu, Wen Liu, Jian Liu, Siyu Chen, and Xingbo Zhao. Feed restriction induced changes in behavior, corticosterone, and microbial programming in slow-and fast-growing chicken breeds. *Animals*, 11(1):141, 2021. [109](#)
- [122] Helen F Yan, Peter M Kyne, Rima W Jabado, Ruth H Leeney, Lindsay NK Davidson, Danielle H Derrick, Brittany Finucci, Robert P Freckleton, Sonja V Fordham, and Nicholas K Dulvy. Overfishing and habitat loss drive range

- contraction of iconic marine fishes to near extinction. *Science Advances*, 7(7):eabb6026, 2021. [20](#), [21](#)
- [123] Xuejie Yi, Donghui Tang, Shicheng Cao, Tao Li, Haining Gao, Tie Ma, Tingting Yao, Jing Li, and Bo Chang. Effect of different exercise loads on testicular oxidative stress and reproductive function in obese male mice. *Oxidative medicine and cellular longevity*, 2020:1–13, 2020. [109](#)
- [124] Zhi-Jun Zhao, Qing-Sheng Chi, Jing Cao, and Ying-Dong Han. The energy budget, thermogenic capacity and behavior in swiss mice exposed to a consecutive decrease in temperatures. *Journal of Experimental Biology*, 213(23):3988–3997, 2010. [128](#)

Vita

Maggie Sullens is the second child of Randall and Tracie Sullens, preceded by her sister, Amanda. Born in Cumming, GA, Maggie attended North Forsyth High School where she participated in a dual-enrollment program her junior and senior year with the University of North Georgia. After graduating in 2017, she continued full time at the University of North Georgia in Dahlonega, GA until receiving a B.S. in Mathematics in Spring 2019. In the Fall of 2019, Maggie moved to Knoxville, TN to begin her Ph.D career in Mathematical Ecology. She completed the requirements and received a M.S in Mathematics in 2021 while enrolled in the Ph.D program. Under guidance from her advisor Dr. Nina Fefferman, Maggie developed research skills in mathematical modeling involving biological and behavioral systems and found her love of applying mathematical tools to a variety of different applied questions. She completed her Ph.D in 2024.