The Effect of Prey Size on Emergent Predator Group Sizes: An Agent-based Model

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Abstract

Group dynamics such as cooperative hunting is an essential behavioural feature among many types of predators. Yet few current models of predator-prey dynamics address how these groups emerge from complex interactions between heterogeneous predators. We introduce an agent based model which uses cooperative hunting in an evolutionary game theory setting, to ask how the size of the available prey relates to the emergent cooperative behaviour and group sizes. The model outputs suggest that an increase in prey size will lead to more cooperative hunting strategies among predators, which in turn results in larger group sizes. Additionally, the model's density function for group sizes presumably follows a power law in it's higher limit tail, thus very large groups can arise. We discuss how future agent based models can be elaborated in complexity to gain more ecologically insights.

1 Theoretical Framework

In this section we will discuss the preexisting predator-prey models, to motivate our research.

1.1 Cooperative hunting in predators

Population densities and hunting behaviour among predators, such as lions, inevitably depend on the availability of prey Schaller (1972). Furthermore, living and hunting in groups may benefit individuals through increased hunting efficiency and energy conservation (Geritz and Gyllenberg (2013)). This is seen in lions, where capture efficiency increases with group size (Caraco and Wolf (1975)). Group sizes among social predators balance the collective hunting abilities and the competition among group members (Nudds (1978)). Within species of predators, large variation is found in group sizes (Griesser et al. (2011)). Among other things, this largely depends on availability and quality of prey, in terms of e.g. body size, since larger prey can satisfy the energy demands of a larger pack/pride (Schaller (1972)). Additionally, individual abilities of group members may also affect group size greatly (Wang et al. (2016)). In fact, the stability of many ecosystems relies on group dynamics and, as such, a focus on cooperative group behaviour is valuable when modelling how predator-prey populations interact (Fryxell (2007)). Nevertheless, previous models of predator populations and hunting behaviour do not account for group behaviour.

1.1.1 Lotka-Volterra Model and the Wolf-Sheep model

The Lotka-Volterra model (Lotka (1920); Volterra (1928)) has been successful in modelling how interdependencies between two species affect fluctuations in their populations sizes. However, the Lotka-Volterra model assumes absolute homogeneity of individuals within a species, and that predators and prey are evenly distributed in their environment. Meanwhile, predators and prey may vary both physiologically and behaviourally (e.g. body size, hunting ability, age), and are rarely distributed evenly. The model consists of partial differential equations with two variables. A variable x for the prey population and a variable y for the predator population Volterra (1931):

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad \frac{dy}{dt} = \delta xy - \gamma y$$

Regardless of its shortcomings in terms of group behaviour, the Lotka-Volterra equations produce accurate predictions of natural population fluctuations Volterra (1931).

The Wolf-Sheep model (Smith and Conrey (2007)) recreates these fluctuations in an agent-based model paradigm with a certain set of stable parameters. It models wolves and sheep as moving agents who reproduce, die, eat or get eaten. The model introduces space into the investigation of population sizes. Nevertheless, it has no feature of cooperative hunting.

1.2 Evolutionary Game Theory

To further investigate the evolutionary benefits of predator group behaviours and the dynamics regulating these behaviours, it is useful to assess the utility of cooperating for each individual under different circumstances. This game theoretical perspective was applied to predator hunting behaviour by Packer and Ruttan (1988). They assessed the success of two hunting strategies, namely 'Cooperating' and 'Cheating', assuming these were evolutionary stable, i.e. the entire population converges to either strategy.

'Cooperating' means that a predator cooperates with other cooperating predators around they to hunt and share the prey. 'Cheating' means that a predator waits to see if another predator attacks the prey first, and will take some of the dead prey after the attack is finished. However, if there is no such other predator that attacks the prey first, then one predator amongst the cheaters (chosen randomly) will hunt the prey alone.

The authors compared the predictions for homogeneous strategies of 'Cooperating' or 'Cheating' among different types of predators against real data (see Figure 1). When group size is plotted against the group hunting success, the data lies between the model predictions of the two homogeneous strategies.

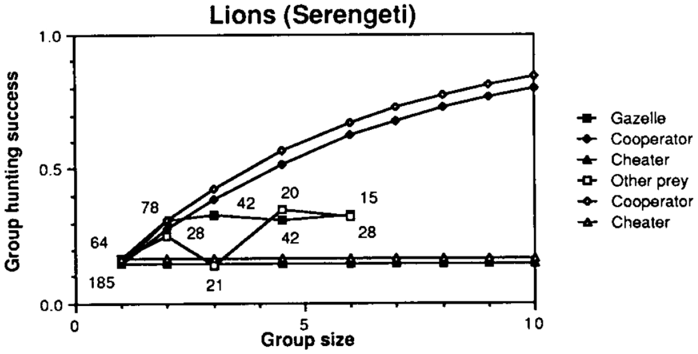

Figure 1: Example of a prediction from Packer and Ruttan (1988)

This suggest that the hunting among predators does not consist entirely of cooperative hunting or the scavenging strategy of cheating. Rather, individuals of the population may vary their hunting behaviour using a dynamic mixed strategy based on their environment and experiences.

1.3 Previous findings on animal group sizes

In Computational Science, research has been conducted into how animals should choose whether to join a group or not. Daniels et al. (2017) modelled the fight sizes of captive pig-tailed macaques. They found that models which consider monkeys joining a fight as an independent event (only depending on their previous fighting frequency), give zero probability to the forming of large groups (see Figure 2). However, models that include social interactions (such as the Equilibrium and Dynamic model) give positive probabilities (however small) to the forming of large fighting groups. This heavy tail follows existing data.

Another model which tries to capture this phenomenon is from Bonabeau et al. (1999). They claim that heavy-tailed group size distributions are a generic phenomenon, although it is often neglected in the literature. The predictions in their model are validated against group-size distribution data in African Buffaloes, which show fat-tail behaviour (namely groups of size > 1000 occur).

We are interested in investigating whether our model outputs replicate similar fat tail distributions.

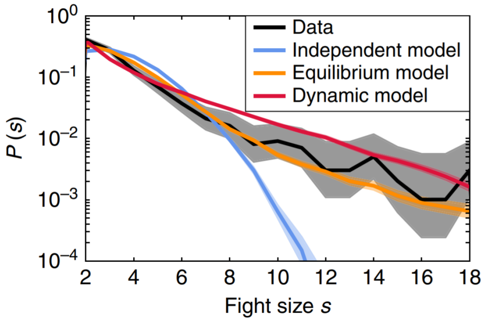

Figure 2: Results from Daniels et al. (2017)

Model Overview

2 Purpose

The purpose of the current model is to advance the understanding of how prey size affects the cooperative hunting amongst predators. Specifically, we sought to design a model which could answer the question of *how the size of prey affects the emergent group sizes of predators hunting cooperatively.* The model is inspired by the Wolf-Sheep model by Smith and Conrey (2007) with an evolutionary game theory approach, but address local patters of cooperation as an effect of spatial distribution and heterogeneity among agents. The model may offer insight to the field of zoology by simulating how group sizes can change and emerge from local differences in agents and from global differences like size of prey.

Why an Agent-based Model?

We employed an agent-based modelling paradigm to answer our research question for five key reasons, which will be elaborated in the following sections. Using this method we seek to address the facts that predators have individual differences (i.e. are heterogeneous agents). Also, that they earn from their different experiences which enables them to adapt their behaviour to suit the state of their environment (such as the size of available prey). This learning and adapting depends on complex, non-linear interactions with other predators, who have all made their own adaptions to the environment. Furthermore, as space is a crucial component since cooperative hunting requires some clustering by the agents. Moreover, we see this as prey are not necessarily equally available throughout the environment. It is due to these local differences in hunting behaviour amongst the agents and throughout the space that we see this emergent behaviour. These facets of the research question at hand render equation-based models insufficient. An agent-based design allows us to address these features of predators, their environments and interactions.

3 Entities, State Variables and Scales

We will first describe the entities in our model, namely the environment and the agents. For each type of agent we will expand on the corresponding parameters of our model, the state variables. When relevant, we will address the related scales and units.

3.1 Entities

Environment

The environment is a 20×20 multi-grid torus from the python library Mesa from Project-Mesa-Team (2018). The discrete space was chosen to mimic the local surroundings and movements of predators and prey and to reduce computational costs. The environment is similar to the Wolf-Sheep model as described in Smith and Conrey (2007).

Agents

There are two distinct types of agents in our model, namely predators and prey. See section 3.2 for parameters and variables, and section 4 for details on agent behaviour.

3.2 State Variables and Scales

For the state variables we will make a distinction between fixed *settings* (settings that are consistently used in the analysis and remain fixed during sensitivity analysis), uniform *parameters* for agents (which are varied at the beginning of each analysis, but remain the same during one run) and non-uniform *attributes* (which are initialised differently for each agent and are updated each time step). We will indicate the categories with the superscripts s, p, a respectively. The state variables can be seen in Table 1 and we will expand on them in the relevant sections. The scales used during the sensitivity analysis can also be found in this table. For parameters, we first describe the initial setting, and then the bounds within which we sampled. For a detailed description of the implementation of the parameters, see the section 4 .

Table 1: State Variables in the model

	State Variable Name	Definition	For p: (initial value − bounds) For s: the setting For a: the possible values
Environment	Defection Gain^p	Utility gained by defecting predators.	$2-$ $[0, 3.6]$
	Grid Size^s	The dimensions of the grid	20×20
	Carrying Capacity^s	Max number of prey and	
		0.2·max number of predators in the environment	1000
	Initial prey/predator^s	The initial number of prey and predators	500/500
Agent: Prey	Prey Value^p (PV)	Utility that can be passed on to predators	9 - $[5, 24]$
	Reproduction Rate^p	The rate at which a prey will reproduce asexually	$0.38 - [0.1, 0.6]$
Agent: Predator	Energy Level^a	How much energy the predator has	$[0, \infty]$
		(If a predator has energy below 1, he will die)	
	Memory^a	A list appended memory of each cooperating utility	$[0, \text{Prey Value}]$
	Memory Window^p	How many memories used to determine their strategy	$14 - [2, 21]$
	Initial Memory Size^s	How many memories a predator receives upon initialisation	5
	Hunting Ability^p	The probability that a predator successfully hunts a prey	0.31 - $[0.15, 0.58]$
	Predator Death Rate^p	The probability that a predator dies	$0.165 - [.1, .25]$
	Mating Threshold^p (MT)	The amount of energy a predator needs to reproduce	$\frac{\text{PV}}{1.10} - [\frac{\text{PV}}{9}, \frac{15 \cdot PV}{9}]$
	Mating Cost^p	The energy cost for a predator to reproduce asexually	$\frac{\text{MT}}{2.30} - [\frac{\text{MT}}{8.2}, \frac{\text{MT}}{1}]$
	Vision^s	Radius of Moore Neighbourhood to select prey from	1
	Step Cost^s	The amount of energy it takes a predator to take a step.	1

Environment

The environment has four state variables. The Defection Gain parameter denotes the amount of energy a predator receives when choosing to defect upon encountering a prey. The Grid Size, Initial Number of Prey and Predators and Carrying Capacity are fixed settings. The Carrying Capacity was added to control computationally heavy exponential growth of the agents. The number of predators is controlled by putting a mating stop when 5 times the carrying capacity is reached [1]. We refer to the Ricker model which is mentioned in the next section as well as being fully described as a submodel of our model in section 8.1. This is a constraint on the environment as it limits the amount of prey being able to be produced.

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[1] This limitation of the amount of predators will not influence the sensitivity analysis. When this amount of predators is reached, no prey will be left so the outputs (ratio predator/prey, ratio cooperators/defectors, average group size) will not change if the predators grow even bigger, hence the variance will not change.

Prey

The prey are homogeneous agents. The Prey Value is the amount of energy a prey yields when it is eaten by a group of predators. So it represents the actual size or biomass of a prey. The Prey Reproduction Rate is the probability that a prey reproduces. This probability changes each time step in accordance with the Ricker Equation (Ricker (1954)), see section 8.1.

Predators

The predators are heterogeneous agents, due to the individually differing attributes Memory and Energy Levels. The memory holds the results for previous hunts (see section 6.3) and the Energy Level stands for the amount of Energy a predator has. The Memory Window is a parameter that determines how many memory slots a predator can access, see section 6.4. The Initial Memory Size determines how many initial values are stored in the predator's memory. The Hunting Ability is the probability that a predator successfully hunts a prey (see section 8.2). The Predator Death Rate is the probability that a predator dies at the beginning of each time step. For robustness of the model, the Mating Threshold is related to the Prey Value. This is to prevent parameter settings where the Mating Threshold is very high in comparison to Prey Value (or vice-versa) resulting in the fact that predators almost never mate (or mate way too often). Also, the Mating Cost is always below the Mating Threshold. This prevents predators from dying as a result of mating. The Vision and Step Cost are self explanatory.

4 Process overview and scheduling

4.1 Prey step

When the prey is activated it first checks if there are predators who want to attack it. If there are cooperators amongst these attackers, there is a possibility that the prey will be successfully hunted. This is determined by the game play, fully described in Section 9.2. If the prey is killed, it will be removed from the grid, which terminates the step of this prey. Its value is added to the Energy Levels of the attacking predators. If the prey survived or if there are no predators attacking it, then the prey will make a random move of one step, by randomly choosing a grid cell in its Moore neighbourhood with radius 1. Finally, it will conditionally reproduce with the probability R_t, which is determined by the Ricker model, see Section 9.1. As the reproduction rate is a random chance, if at this step the random number is high enough, then the prey reproduces. If a prey reproduces, its offspring will be placed on the same grid cell. A schematic representation of the prey step is shown in Figure 3.

4.2 Predator step

While the prey only die when they are killed, a predator dies either randomly with probability Predator Death Rate or when their Energy Level becomes lower than 1. In these cases the predator is removed from the grid and its step is terminated. If the predator is still alive it will choose a strategy (Cooperate or Defect) based on its memory, see section 5.4. Then the predator randomly moves to a new position, by randomly choosing a cell from its Moore neighbourhood (with a radius of one). During this move the predators Energy Level is lowered with the Step Cost (i.e. 1). If there is prey around, the predator will randomly pick a prey from its Moore neighbourhood with radius Vision (i.e. 1). The predator is now considered an attacker of this particular prey, and will attack during the game play once the prey is activated in the next time step (see section 8.2). During this attack they will use the strategy they have just chosen. If there is no prey around, the predator is not able to select a prey and therefore is unable to hunt. This means the predator will not gain any energy during the upcoming time step. Lastly, predators reproduce asexually if their Energy Level is higher than the defined Mating Threshold. Reproducing will lower the predators Energy Level with the amount defined by the Mating Cost. If a predator reproduces, its offspring will be placed on the same grid cell. A schematic representation of the predator step is shown in Figure 4.

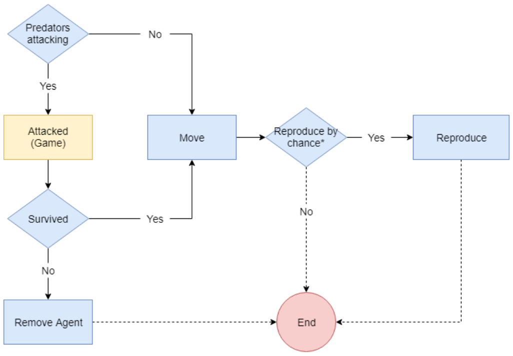

Figure 3: Prey Step

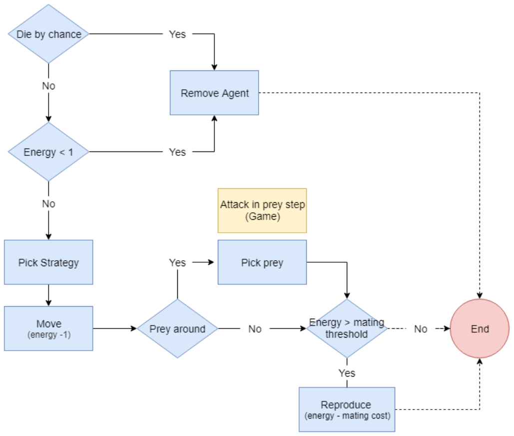

Figure 4: Predator Step

4.3 Scheduler

Time is modelled by discrete steps in our model. During each time step the prey and predator agents are randomly activated by breed; first all the prey are activated in a random order, after which the same happens to the predators[2]. The order of activation of single agents within a breed is random according to the Mesa RandomActivation scheduler (Project-Mesa-Team (2018)). Hence we call our scheduler RandomActivationByBreed (Roy (2019)). See Algorithm 1 for the pseudocode of this scheduler.

This scheduler was suitable for our research because the two agents, prey and predator, are activated one at a time but still relate to one common random scheduler. We need the breeds to be activated one at a time, because we want that every predator has chosen a prey before the game is played (see section 8.2).

Algorithm 1 RandomActivationByBreed

```
$D \leftarrow$ empty dictionary
procedure ADD AGENT TO SCHEDULER
    $D[agent.class][agent.unique\_id] \leftarrow$ agent
procedure STEP
    for agent_class in D do
        $agent\_keys \leftarrow$ list(D[agent_class].keys())
        shuffle(agent_keys)
        for agent_key in agent_keys do
            $D[agent\_class][agent\_key].step()$
```

5 Design Concepts

As previously stated, the purpose of this project is to investigate how the size of prey will affect the emergent group sizes of cooperatively hunting predators. It relies on population dynamics and evolutionary game theory frameworks, using an agent based model to address gaps in the literature.

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[2] Since the prey are activated first, there won't be any attacking predators in the first time step of our model. In the final time step (when the model terminates), the predators are denied a chance to hunt for their chosen prey. Because we always run the model 150 steps, these disturbances have no influence on the outcome, as we could have ran it 151 steps, getting similar results.

Hypothesis

In accordance with previous findings, i.e. that prey biomass correlates with predator group size Schaller (1972), we hypothesise that a larger prey size will teach heterogeneous predators that group hunting (cooperation) is more rewarding than hunting small prey alone (defecting). As prey size increases, predators are dividing a larger sum amongst them making cooperation more beneficial, as well as making the chance of a successful hunting more likely. Conversely, if the prey size is too small, this would entail that the predators' strategies would gravitate towards defecting. We predict that this will also depend on the ratios between predator and prey populations. The frequency of encountering both types of agents will affect the hunting success.

Additionally, we hypothesise that our model will show the probability of being in a group of a certain size is non-linear, as previously mentioned in Daniels et al. (2017) and Bonabeau et al. (1999).

5.1 Emergence

Different group sizes of cooperators are not built into our model, but are asymmetrically emergent properties of the interaction between heterogeneous agents, in patterns which cannot be extrapolated from individual agent characteristics. An agent's memory of cooperative success depends, for one, on the previous choices of the other agents, which in turn uses their memory. As the strategies of the agents rely on previous experiences, which in turn has been affected by the other agents,local differences in cooperation are expected to occur under varying states of the system.

5.2 Adaptation

Predators have the ability to adapt to the demands of the environment in the form of learning-based strategic decision-making (see section 5.4). Thus, the state of the environment and the surrounding agents influence the strategic preferences of predators. As such, predators can optimise individual energy levels through the latent knowledge of the system state.

5.3 Objectives

The objective of predator activity is to sustain a stable energy level, where an energy surplus results in reproduction and death. Therefore, the fitness of a predator relates to how well its mixed strategy maximises its energy levels. The evolutionary analogue to this objective is for the individuals to survive and pass on their genes through adaption to the environment.

5.4 Learning

Each predator has a memory consisting of utility gained from every game where it cooperated. Let n denote the Memory Window parameter. n determines the scope of access to the memory (e.g. 14 latest entries). When a predator reproduces, the offspring inherits its memory to implement an evolutionary component. The Defection utility is defined as the Defection Gain, as this represents a small prey, which is guaranteed to be hunted successfully.

Predators use their memory to update their mixed strategy between Cooperating and Defecting. The mixed strategy is derived as follows:

$$Pr(\text{Cooperate}) = \frac{\text{Average Cooperation utility}}{\text{Average Cooperation utility} + \text{Defection utility}}$$

Where Average Cooperation utility is the average over the last n entries in the memory. When the average Cooperate utility is equal to the Defection utility, then the predator has an equal chance of playing Cooperate or Defect. When the average Cooperation utility becomes larger than the Defecting utility, then the predator will have a higher probability of Cooperating. With this updated mixed strategy, a random chance determines the whether the Cooperate or Defect.

5.5 Prediction and Sensing

Predators sense their environment partly through vision of adjacent prey, and partly through memory. That is, while vision does not convey any information about the amount of predators around, this is implied by the average cooperation success. Predators use this information to predict the expected utility of cooperating. If too few predators are around for each game, a predator will learn this through a lower success rates. Prey do not have vision, but store information about the predators who chose them for the current game.

5.6 Interaction

There are two types of interaction in our model. Firstly, at each step each predator picks a prey within their visual field, see section 4.2 for a detailed description. Secondly, predators and prey interact whilst playing the game. Predators with the strategy 'Cooperate' hunt together and try to kill the prey. For more information see section 8.2.

5.7 Heterogeneity

Prey are completely homogeneous and the predators have the attributes Energy Level and Memory that are different for each agent. Detailed information can be found in section 3.2.

5.8 Stochasticity

Stochasticity is implemented in many processes in the model. In Table 2 all the stochastic steps can be found.

Process	**Stochasticity**
Scheduler	See section 4.3
Agent move	See section 4.1/ section 4.2
Choosing strategy	See section 5.4
Hunting	See section 8.2
Prey reproduction	See section 4.1
Predator dying	See section 4.2
Memory initialisation	See section 6.3
Energy Level initialisation	See section 6.4
Initial agent position	See section 6.2

Table 2: Overview of collected observations

5.9 Collectives

During a game or hunt, predators may join an ad hoc cooperative group in which they hunt collectively. A group's collective probability of killing prey increases with the number of cooperators in it, and the collective utility of a successful hunt is divided between it's members. The collectives are formed ad-hoc and disperse after each game. An example of this can be seen in Figure 5.

5.10 Observation

The scheduler RandomActivationByBreed from Project-Mesa-Team (2018) allows for data collection at the end of each step. The data collector is called upon and registers observations at the end of each run of the model. The observations collected are listed in Table 3. Note that in Table3 the average group size we also include groups of size 1, a single cooperator.

6 Initialisation

In order to describe the initial state of the world, we need to take close look at the initial values for the parameters, the settings and the predator's attributes (Memory and Energy Level).

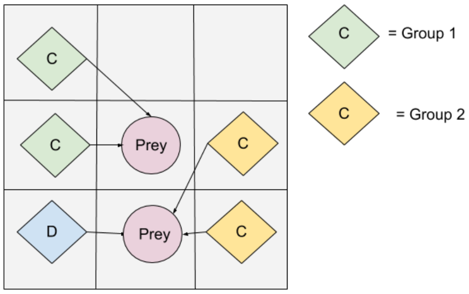

Figure 5: The notion of a group in our model

Observation	Meaning of observation
Prey count	Total number of prey at the end of a step
Predator count	Total number of predator at the end of a step
Ratio Prey/Predator	Ratio between the amount of prey and the amount of predators
Ratio Cooperators	Ratio of cooperators as a fraction of total number of predators
Average group size	The average group size at the end of a step
Group size count	Number of groups of sizes 1 until 21+ (one observer for each size)

Table 3: Overview of collected observations

6.1 Parameters and settings

For the initial values of the parameters and the settings, we refer to Table 1. We chose these parameters and settings because they provide us with a stable regime, that can be seen in Figure 6. During sensitivity analysis, the settings remain the same in each run. However, we varied the parameters over the bounds that are given in Table 1.

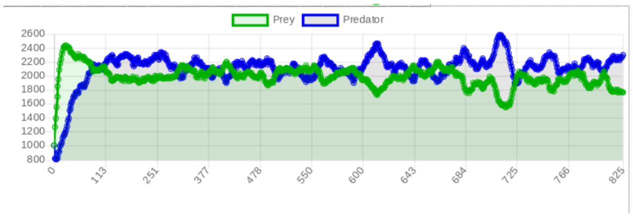

Figure 6: Predator and Prey populations with the initial parameters

6.2 Initial placement of agents on multigrid

Upon initialisation, a fixed number of predators and prey are placed on the multigrid, this number is determined by the setting Initial Prey/Predator. Their location is chosen randomly. Two random integers are chosen between zero and twenty. The first number denotes the agent's place on the x-axis, the second one the place on the y-axis. These coordinates determine the cell which the agent is initially placed on.

6.3 Memory

Upon initialisation, each predator is attributed an individual memory. We define n as the setting: Initial Memory Size (i.e. $n = 5$). Each predator receives n random numbers in their memory that are drawn from a truncated normal distribution over the range [0, Prey Value] that is centred at the mean $\mu =$ Prey Value $\times$ Hunting Probability. This distribution is depicted in Figure 7. We chose this distribution because is mirrors the fact that a predator has an expected utility of μ when hunting alone, and when hunting (alone or in a group) their utility will always be a value between 0 and the Prey Value.

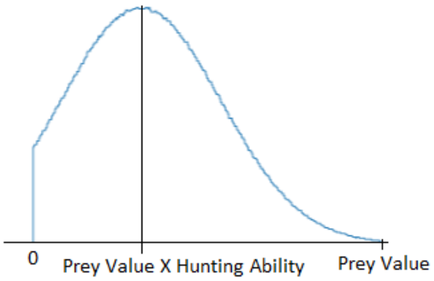

Figure 7: Truncated Distribution to initialise Memory

6.4 Energy Level

When a predator is placed on the multigrid, his Energy Level is initialised by picking a random integer in the range $(\min\{2, \lfloor \text{Mating Threshold} \rfloor\}, \lfloor \text{Mating Threshold} \rfloor)$.

We want the Energy Level to be at least 2, because it prevents predators from dying in the second step if they didn't hunt (then their Energy Level still will be at least 1) and because now predators must play the game at least once before they are able to mate. This way each offspring will inherit a memory (thus a mixed strategy) based on at least one actual utility obtained by playing the game.

We can't implement the lower bound of the range to be 2, because there are some parameter settings where the Mating Threshold is below 2. In that case, we can't pick an integer in the range $[2, \lfloor \text{Mating Threshold} \rfloor]$. We catch this impossibility by defining the lower bound to be the minimum of those two values.

7 Input data

Our agent-based model does not use input data to represent time-varying processes.

8 Submodels

There are two submodels in our agent based model. These are the Ricker Model and the game that is played.

8.1 Ricker Model

We implemented the Ricker Equation to compensate for two model simplifications. Firstly the prey only die when they are eaten by the predators, secondly they do not consume resources, as there is no notion of food for the prey in this model. The Ricker Model was created to model the behaviour of the populations in fisheries. It models how reproduction rates of fish decrease if the amount of fish grows too big (and vice versa, the reproduction rates increase if the amount of fish is too little). The Ricker equation is as such:

$$R_t = exp[R_0(1 - \frac{N_t}{K})] - 1$$

This equation takes as inputs the Prey Reproduction Rate R_0, the population at time t denoted by N_t and the carrying capacity K and outputs the corresponding reproduction rate at time t, namely R_t. When N_t tends towards the carrying capacity, the reproduction rate at this time step becomes closer to zero. Alternatively, if an agent population at a given time step is tending towards zero, the reproduction rate will tend towards $e^{R_0} - 1$, which is always larger than R_0. Therefore a small amount of agents increases the chance of reproduction. Implementing this equation results in the well known S-curve for the population of preys in absence of predators, we see this in Figure 8.

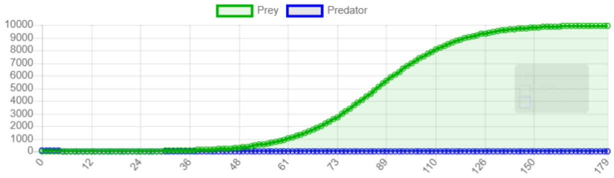

Figure 8: The Ricker Model Operating in our Model

8.2 Game Play

If a prey has k (with $k \geq 1$) predators that have chosen them, then game play occurs. The k predators already determined their strategies in the predator step (see section 4.2). Say there are m cooperators and thus $k - m$ defectors. The $k - m$ defectors will get the utility of the parameter called Defection Gain. The m cooperators will then try to attack the prey. The parameter Hunting Ability (HA) is their probability of hunting successfully. When hunting together, the cooperator's total hunting ability is the probability $1 - (1 - HA)^{m}$[3]. If they are successful in hunting the prey, then they will split the prey value amongst the m cooperators. Hence the utility gained will be $\frac{\text{Prey Value}}{m}$. This utility gained from a successful hunt will be appended to the cooperating predator's memory and it will be added to the Energy Level of each cooperating predators. If the cooperators are unsuccessful, (thus the probability was larger than the hunting ability), then all the cooperators get a utility of zero, which in turn will be appended to the memory. The expected utilities for the predators are:

$$EU(D) = \text{Defection Gain} \qquad EU(C) = (1 - (1 - HA)^{\#\text{ cooperators}})\frac{\text{Prey Value}}{\#\text{cooperators}}$$

The defectors append nothing to their memory, but the Defection Gain is appended to their Energy Level.

9 Results

During our research we looked into the cooperative hunting behaviour relative to prey size. We will show two main results, namely that cooperation occurs more when Prey Value rises, and that the amount of predators in a group follows a power law distribution.

9.1 Cooperative hunting vs. Prey Value

We ran a detailed OFAT for only the parameter Prey Value, to see how cooperative hunting reacts to varying Prey Values. The bounds for Prey Value were $[5, 18]$ in which the model shows a stable regime, the other parameters where set at their initial settings, as specified in Table 1. We took 40 samples and performed 25 replicates for each sample with 150 steps. Figures 9 and 10 feature how cooperation increases together with Prey Value. That is, the ratio of Cooperators grows from 0.1 to 0.45 and the Average Group Size grows from 1.35 to 1.55. This means that when Prey Value is high, almost half of the predators choose to cooperate, which results in the growing average group size. Moreover, we see that as Prey Value increases, that large groups (groups bigger than size 3) occur more frequently. In Figures 11 and 12 this trend is shown for groups of size 3 and 6. Groups of other sizes (up to size 21) show similar trends.

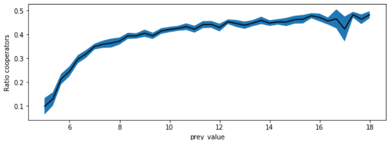

Figure 9: Ratio Cooperators

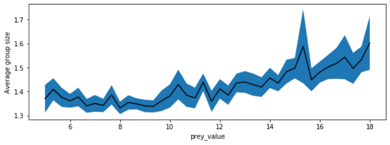

Figure 10: Average Group Size

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[3] The probability of failure is $1 - HA$, the probability of all m cooperators failing is $(1 - HA)^m$ and the probability of the group succeeding is $1 - (1 - HA)^m$

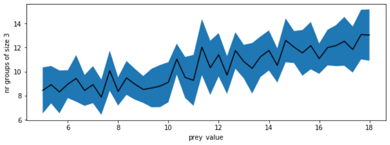

Figure 11: Groups of size 3

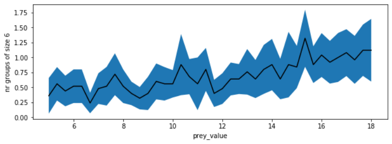

Figure 12: Groups of size 6

Note that we can only talk about trends. In the figures the means at step 150 over the 25 replicates of each observable are displayed by the black line. The blue area stands for the variance.

9.2 Group sizes follow a power law distribution

We considered three Prey Values, namely 6.5, 9 and 20. We ran the model 1000 times (150 steps per iteration) with the previously introduced initial parameters and the separate Prey Values. After each run, the amount of predators in each group was recorded. Finally we plotted the counts per group size against the group size in a log-log plot, which can be seen in Figures 13, 14 and 15. As the log-log plots descend linearly in all of these figures, we believe that the group sizes follow a power law distribution, because this is typical behaviour of such a distribution. This ‘fat tail’ results in the fact that very big groups can form in our model.

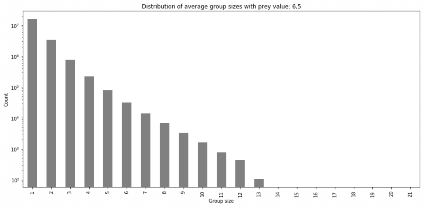

Figure 13: Prey value: 6,5

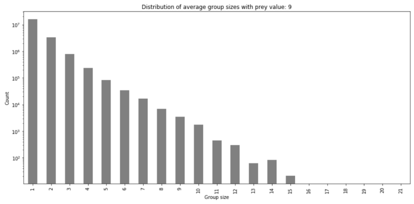

Figure 14: Prey value: 9

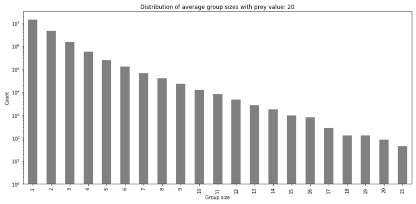

Figure 15: Prey value: 20

As can be seen in above figures, the higher the prey value, the more often large groups are formed. While for a Prey Value of 6.5 the group sizes barely exceed a maximum of 10, for a Prey Value of 20, the group sizes descend very slowly, indicating many groups of size ≥ 21. We conclude that the width of the fat tail is influenced by the Prey Value.

10 Sensitivity Analysis

In order to fully understand the uncertainty from the output of our model we conducted both global and local sensitivity analysis in order to full understand the uncertainty of the inputs of our model.

10.1 Local (OFAT)

For investigating the effect of the different parameters on the outputs of our model, and especially the average group size, One-Factor-At-A-Time (OFAT) sensitivity analysis was used. The method consists of selecting a parameter setting and varying every parameter one at a time, while keeping the other parameters set. This sensitivity analysis allows to reveal a relationship between the output and the parameter, it for instance identifies tipping points.

For the analysis we considered 8 parameters, with the initial parameter setting as specified in Table 1. For every parameter we had 20 equidistant values within the bounds as specified in Table 1, and 10 replicates per parameter value. We ran the model for 150 steps each iteration. The three interesting outputs we considered are Ratio Predator/Prey, the Ratio Cooperators and Average Group Size. In this section, we highlight the most important relations that were found. For a full overview, we refer to Appendix A.

Average Group Size

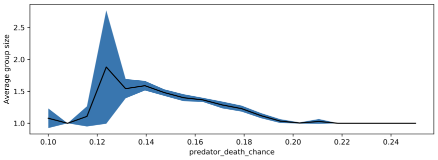

Figure 16: Predator Death Rate

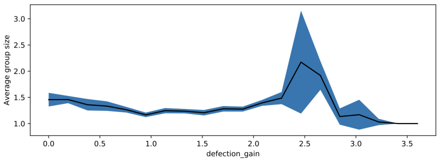

Figure 17: Defection Gain

The Average Group Size was found to be effected interestingly by the Predator Death Rate and the Defection Gain. As we can see in Figure 16, the Average Group Size peaks at a low Predator Death Rate of 0.12. Intuitively this makes sense, since the less predators die, the more predators are able to group together. Finally, the Defection Gain shows interesting behaviour, in which there is a sweet spot around 2.5, which contributes to a higher Average Group Size.

Ratio Cooperators

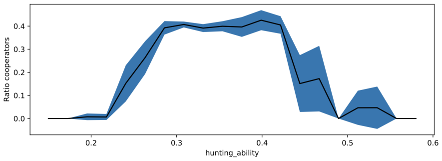

Figure 18: Hunting Ability

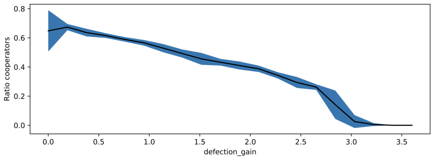

Figure 19: Defection Gain

The Ratio Cooperators was found to be effected interestingly by the Hunting Ability and the Defection Gain. As we can see in Figure 18, the Ratio Cooperators is at a stable peak at intermediate levels of the Hunting Ability. When the value of Hunting Ability is higher, the predators have a lower need to cooperate. Figure 19 shows that the Defection Gain shows a linearly negative relation to the Ratio Cooperators. The predators, when gaining more from defecting, will logically tend to cooperate less.

Ratio Prey/Predator

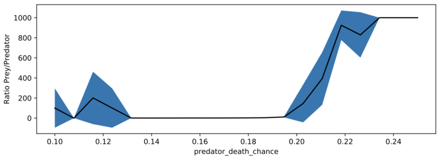

Figure 20: Predator Death Rate

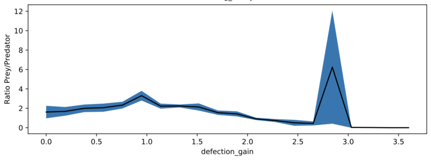

Figure 21: Defection Gain

The Ratio Prey/Predator was found to be effected interestingly by the Predator Death Rate and the Defection Gain. Figure 20 shows that the Ratio Prey/Predator is highest from a Predator Death Rate of

0.21 on. At this point, the predators die out faster which leads to a high relation between the prey and predator. The Ratio of Prey to Predator (calculated by prey divided by predator) is less directly influenced by the Defection Gain which is shown in Figure 21. The ratio seems to get the highest values when the Defection Gain is just under 3.

Tipping Points

Lastly we want to identify some tipping points. Looking at the graphs in Appendix A, we see that for our initial settings, the model outcomes are very stable when the Predator Death Rate is between 0.14 and 0.19. Going outside these bounds makes the model outcomes unstable. The Prey Reproduction Rate shows a tipping point at 0.2. Above this value, the outputs behave stable. The Mating Threshold also shows a tipping point. Above 3 the system shows no interesting behaviour anymore. We see that the system is also stable when the Hunting Ability is above 0.2. Underneath all the predators seem to die out. Finally the Memory Window shows a tipping point at value 7.5. From this value on, predators will survive.

10.2 Global (Sobol)

We also ran a global analysis on our model, using the Sobol method. Sobol is a method to decompose the variance into fractions which can be attributed to the parameters and their interactions. We looked at the first-order sensitivity index for each parameter, which is a measure for how sensitive the model's output is when that single parameter is varied. We also looked at the total-order sensitivity index for each parameter, which indicates how influential a parameter is on the outcome, when it interacts with all the other parameters.

For the analysis we considered 8 parameters, with the bounds as defined in Table 1. We had 20 distinct samples, and 7 replicates, resulting in a sample matrix of $20 \cdot (8 + 2) = 200$ rows. We ran the model for 150 steps each iteration. The three interesting outputs we considered are Ratio Predator/Prey, the Ratio Cooperators and Average Group Size.

Average Group Size

As can be seen in section 9.2, the amount of predators in each group follows a power law distribution. A power law distribution has infinite variance. Therefore it makes no sense to describe the deviation from the Average Group size using variance, (Kreinovich and Kosheleva (2014)).

So unfortunately we can't use Sobol's method to properly analyse the global sensitivity of this output.

Ratio Prey/Predator

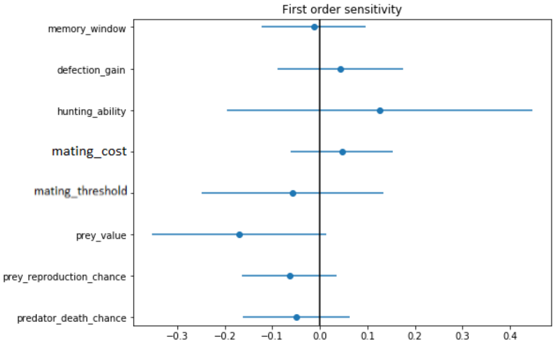

Figure 22: Ratio Prey/Predator first-order index

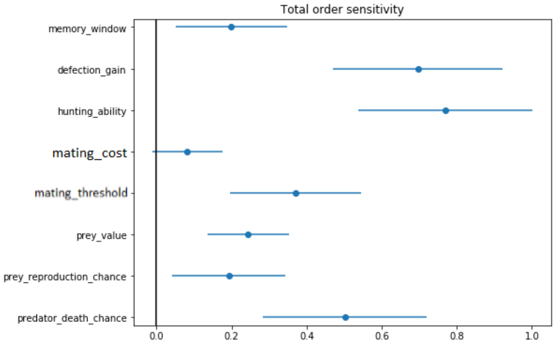

Figure 23: Ratio Prey/Predator total-order index

First-order index

For the Ratio Prey/Predator we see that the Hunting Ability parameter has the highest first-order index. This matches our intuition. When we only vary the Hunting Ability, predators become more or less successful at hunting. For a fixed number of predators this means that the number of prey will be either very high or very low (or somewhere in between), causing lots of variation in the output Ratio Prey/Predator. So when we want to make this output more reliable, it would be wise to first get a proper estimate of this parameter. The model is not very sensitive for variations in the other parameters (except for Defection Gain and Mating Cost).

Total-order index

We see that when we include interaction with other parameters, Hunting Ability and Defection Gain are most influential on the variance of this output. Even the lower bounds of their confidence intervals are above the estimated total-order indices of the other parameters. For the Hunting Ability the same reasoning applies as for the first-order index. The Defection Gain has such a big influence on the output because it has a large influence on the mixed strategy, hence on whether predators cooperate or defect (i.e. whether prey are hunted or not). Observe that the Mating Cost explains almost no variance of the output. So in the case of limited resources, this output can be fixed.

Ratio Cooperators

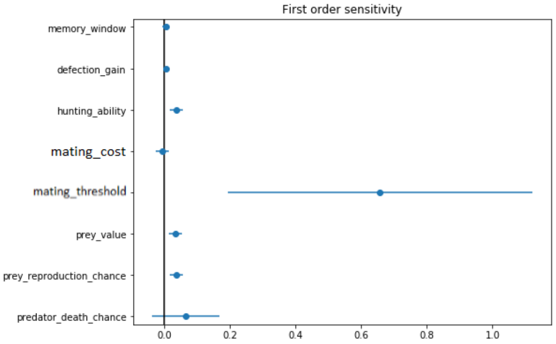

Figure 24: Ratio Cooperators first-order index

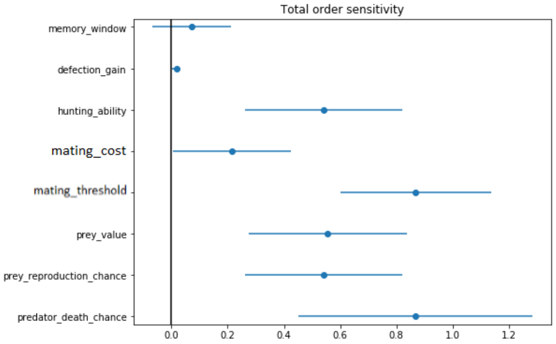

Figure 25: Ratio Cooperators total-order index

First-order index

For the Ratio Cooperators, we see that the parameter Mating Threshold has a very high first-order index, and that the other parameters have low first-order indices. So when parameters don't interact with each other, only the Mating Threshold has influence on the variance of the output. This result is counter-intuitive. The Ratio Cooperators is formed by the choice of strategy from each predator. This choice of strategy has no direct relation to the Mating Threshold, which is only of interest whether a predator reproduces or not. We expected that the first-order index of the Defection Gain would be higher, as this is influential on the choice of strategy. However, this results coincides with our findings from the OFAT analysis. when we look at Figure 19, we see that there is very little deviation from the mean for different values of the Defection Gain.

Total-order index

When we include interaction with other parameters, Predator Death Chance and Mating Threshold are the most influential. According to this Sobol Analysis, the parameter Defection Gain can be fixed, it has (almost) no influence on the variance of the outcome. Again we think this is counter-intuitive, because Defection Gain is a very important factor in the choice of strategy for each predator. See section 12 for a discussion of this result.

11 Validation

Due to time and resource constraints, concise validation of the model has not been possible. Ample data was not available to be used for parameter values that would reflect actual populations.

There is preexisting data on predator group sizes based on prey size, but this is generally not very consistent, and varies between predator types. Thus, to validate in this way we would need to collect our own data, which was not possible.

A second potential method of validation could be to validate our model against yet existing similar models. No existing model to our knowledge has a similar setup to ours, nor looks at varying prey sizes and their effects on predator group size.

However, when we are looking at the validation against other predator-prey models, we can alter our parameters to fit the output as closely as possible to the models in question. We see is that when the model runs in a stable regime it reproduces the Lotka-Volterra equation curves, refer back to Figure 6.

Another way we can validate our model is by the replication of the the power law probability function of larger groups being formed. This distribution was suggested by Daniels et al. (2017) and Bonabeau et al. (1999). We refer back to Figure 2 and show Figure 26 by Bonabeau et al. (1999), where the counts per group size (N(S)) are plotted against the group sizes (S) for African buffaloes. When we compare our power law distribution of group sizes (Figures 13,14 and 15) to these plots, we see that our model aligns with these models (for Figure 26 we need to plot on a log-scale in order to get the same graph).

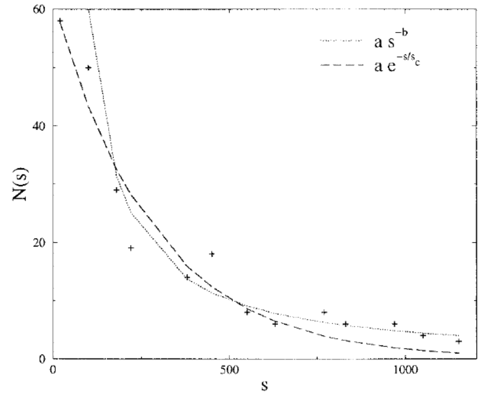

Figure 26: The number of sightings of different herd sizes for African buffaloes

Thus we can see that there is model alignment between our model and both of these models. Hence, we have made an attempt at validating our model this way.

12 Discussion

For the initialisation we had to make important assumptions that are of influence on our model. For instance, we suspect that the design choice to initialise a predator's memory with 5 entries (see section 6.3) is of big influence to the tipping point at 7.5 for the Memory Window (see section 10.1). Also the way the Energy Level (see section 6.4) is modelled is influential on the models behaviour. If we set the lower bound for instance to 0, then the model outcomes are very different.

Our research question and hypothesis only concerned the Prey Value. This intuition was also based on the literature we read, both from biological and computational fields. We saw in the OFAT analysis that there are more parameters affecting the group sizes, other than the Prey Value. This is not what we expected. It would be interesting to explore how the distribution of the group sizes changes according other modifications to the the remaining parameters, in the same way that was done for the Prey Value.

We suspect that the forming of groups is not an independent event in our model. Our outcomes show a fat tail distribution for the groups sizes. Thus, by Daniels et al. (2017) (see Section 1.3), we can infer that complex behaviour of the agents is happening in our model, and that the forming of a cooperative hunt is not just a probabilistic independent event.

Furthermore, this work considers a single predator hunting cooperatively as a group of size one (see section 5.9). The definition which was used for groups is debatable and open for questioning. However, even without groups of size one, the group size distribution would have also shown a fat tail, thus our previous result would be still valid.

In the Sobol analysis (see section 10.2), we saw that the Defection Gain has no influence on the Ratio Cooperators, even when it does not interact with the other parameters. This could be the result of a design mistake. Currently, each predator appends his utility from cooperation to his memory (see section 6.3). So the mixed strategy of each predator (hence the Ratio Cooperators) mostly depends on the utility from cooperation. By tweaking the Defection Gain in order to have a lesser utility for defecting, this could be improved. Especially as from a game theoretic point of view that the defection gain should play a large role in the game play itself and thus the model as a whole.

13 Conclusion and Future Directions

The proposed agent based model replicates predator-prey population dynamics and offers a game theoretical approach to assessing how group sizes among predators emerge. In accordance with our hypothesis our model rendered an increase in both cooperation patterns and in related emergent group sizes. Our methodological paradigm allowed us to simulate these dynamics through heterogeneous agents with a spatial component. Furthermore, we found that the distribution of group sizes was fat tailed.

Future versions of the model and related research could search for interesting dynamics, by incorporating more complexity to gain larger ecological validity. For instance, prey could advantageously be modelled with heterogeneous sizes, so that predators may fight for variable prey. Varying the individual hunting abilities may cause local changes in cooperation patterns. The hunting behaviour can gain larger ecological validity by introducing increasing agent perception and spatial complexity, e.g. allowing a predator to choose and pursue specific prey, and prey may flee a predator. Prey in the wild indeed also group together, which appears important for many ecosystems Fryxell (2007). Further spatial alterations may include a more realistic grid with e.g. grass agents as feeding for the prey, and a grid size which allows larger distances between the agents. Moreover, a valuable extension would be to use real data from specific predators and prey as parameter settings.

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14 Appendix A

In this appendix the OFAT results can be seen for the Average Group Size, the Ratio Cooperators and the Ratio Prey/Predator.

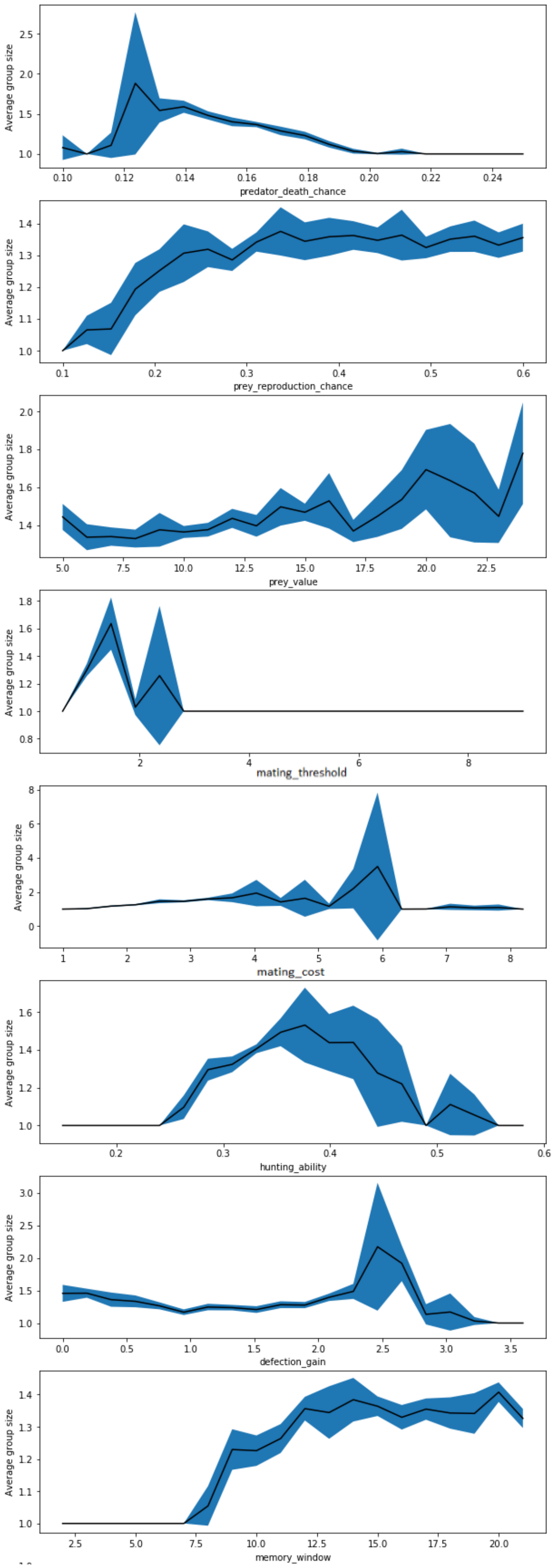

Figure 27: OFAT results for the Average Group Size

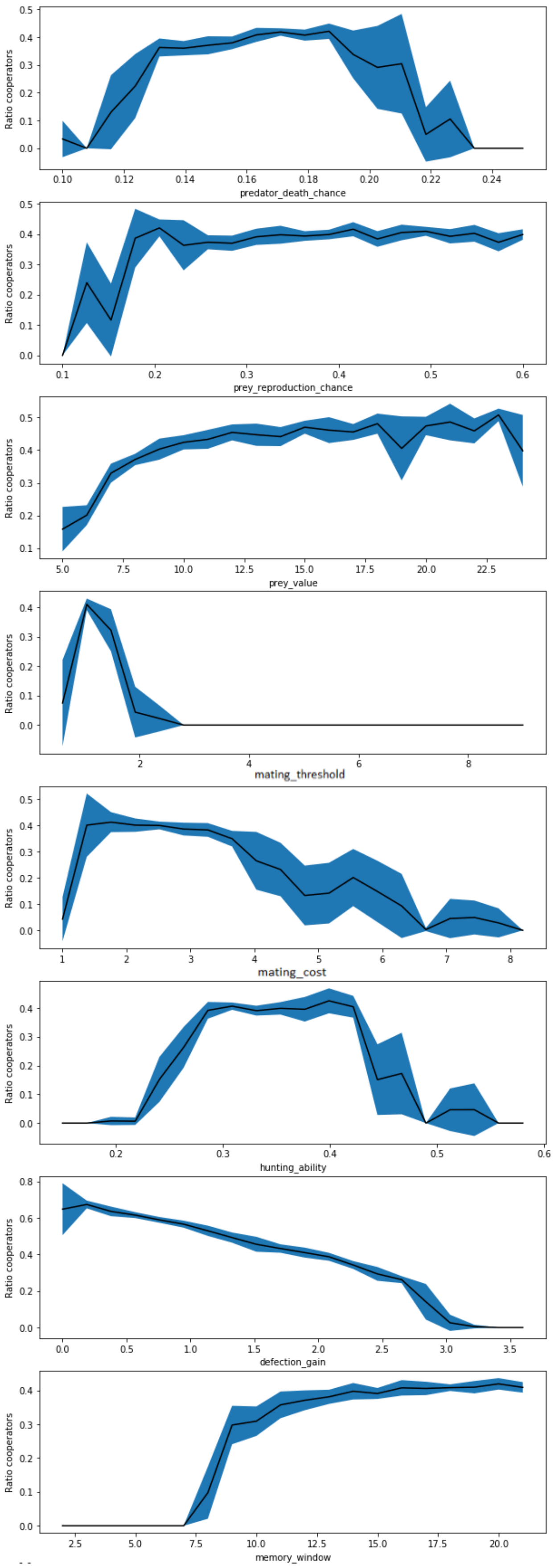

Figure 28: OFAT results for the Ratio Cooperators

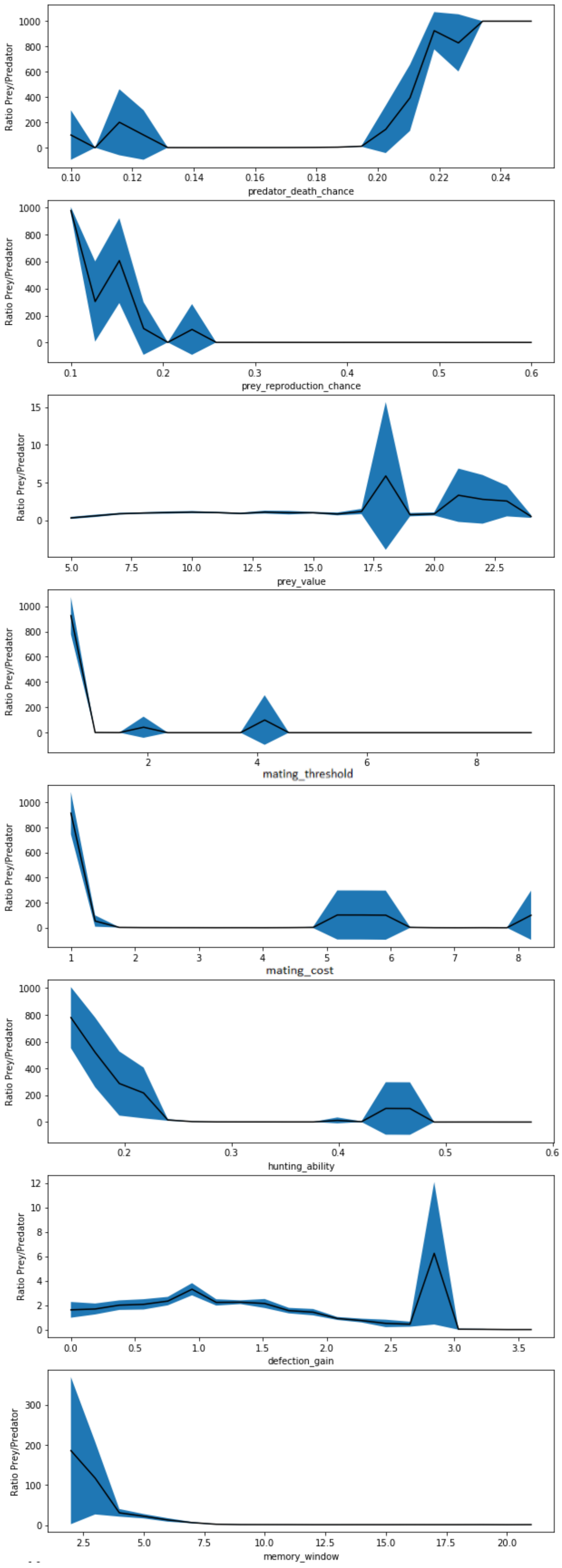

Figure 29: OFAT results for the Ratio Prey/Predator