Developing Multi-agent-based Thought Experiments: A Case Study on the Evolution of Gamete Dimorphism

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Abstract. Multi-agent modeling is a computational approach to model behavior of complex systems in terms of simple micro level agent rules that result in macro level patterns and regularities. It has been argued that complex systems approaches provide distinct advantages over traditional equation-based mathematical modeling approaches in the process of scientific inquiry. We present a case study on how multi-agent modeling can be used to develop thought experiments in order to push theory forward. We develop a model of the evolution of gamete dimorphism (anisogamy), for which there are several competing theories in the evolutionary biology literature. We share the outcomes of our model and discuss how the model findings compare with, and contribute to previous work in the literature. The model clarifies mechanisms that can result in the evolution of anisogamy and offers a much simpler structure that is easier to understand, test, modify and extend.

1 Introduction

The most commonly used approach to model behavior of biological systems involves equational modeling with a focus on describing population-level changes based on population level descriptor variables [9]. Unfortunately, this modeling approach is limited when it comes to adding new variables or incorporating new assumptions because entirely new equations might be needed to capture even small changes [24]. In contrast, multi-agent-based modeling is a powerful approach to model complex natural and social phenomena in terms of simple micro-level agent rules that result in the emergence of macro-level patterns and regularities [21]. In this paper, we draw on Wilensky and Papert's Restructuration Theory and argue that multi-agent-based modeling can be used to develop thought experiments on complex scientific questions for novices to learn scientific domain knowledge easily, as well as domain experts to verify, modify, and even extend these models [24].

We present a multi-agent-based model about the evolution of gamete dimorphism (anisogamy) to make a case for our argument. Anisogamy is the phenomenon of males producing large numbers of small sperm cells and females producing small numbers of large egg cells for reproduction [4]. We believe this topic is a

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good fit for developing a multi-agent-based thought experiment for two primary reasons: (1) there is no universally accepted theory or model in the literature [4,6,16], (2) the bulk of research in this area has been done through equation-based modeling (e.g., [5,12–14]). We begin by reviewing Restructuration Theory in detail. Then, we describe anisogamy and review the literature related to the evolution of anisogamy, as our multi-agent-based thought experiment incorporates and builds on the ideas from the existing evolutionary biology literature. We describe our model's assumptions and agent rules in detail and then present our findings. We demonstrate that our model achieves similar results to those achieved in the literature while increasing access to underlying ideas.

2 Restructuration of Scientific Domain Knowledge Through Multi-agent-based Modeling

Restructuration Theory, as proposed by Wilensky and Papert, describes how disciplinary knowledge can be re-encoded using new representational technologies in a way that can have powerful implications for science, culture and learning [24]. Many such historical restructurations are presented including the restructuration of Roman numerals to Hindu-Arabic numerals. Wilensky and Papert argue that computation offers many new opportunities for powerful restructurations and that multi-agent-based modeling can be used to create many such restructurations [24].

A good example is Wilensky and Reisman's restructuration of models of predation [22]. Traditionally, predator-prey relationships are modeled through differential equations. An example of such models is the Lotka-Volterra models that offer two equations that describe the rate of change in the densities of the predator and prey populations over time [11,19]:

$$\frac{dN_1}{dt} = b_1 N_1 - k_1 N_1 N_2 \tag{1}$$

$$\frac{dN_2}{dt} = k_2 N_1 N_2 - d_2 N_2 \tag{2}$$

In these equations, N_1 is the density of the prey population, N_2 is the density of the predator population, b_1 is the birth rate of the prey, d_2 is the death rate of the predators, and k_1 and k_2 are constants. These equations specify the dependence of the density of each population to one another. When plotted, the model shows cyclical fluctuations between the two populations: increases in the prey population will result in rising predator birth rates and increases in the predator population will result in rising prey death rates. Wilensky and Reisman's attempt to *restructurate* this problem through multi-agent-based modeling focuses on considering prey and predator as agents and describing the agent rules that emerge as population level patterns:

Rule set for wolves *(at each clock-tick)*:

1. move randomly to an adjacent patch which contains no wolves.

2. decrease energy by E_1
3. if on the same patch as a sheep, then eat the sheep and increase energy by E_2
4. if energy < 0 then die
5. with probability R_1 reproduce

Rule set for sheep *(at each clock-tick)*:

1. move randomly to an adjacent patch and decrease energy by E_3
2. if on grassy patch, then eat grass and increase energy by E_4
3. if energy < 0 then die
4. with probability R_1 reproduce

Rule set for grass *(at each clock-tick)*:

1. if green, then do nothing
2. if brown, then wait E_4 clock-ticks and turn green

Wilensky and Papert theorize that multi-agent-based restructurations of such natural phenomena offer three powerful advantages over equation-based modeling in terms of learnability: (1) rules for agents are closer to our intuitive notions of these "objects" as distinct individuals rather than aggregate populations, (2)

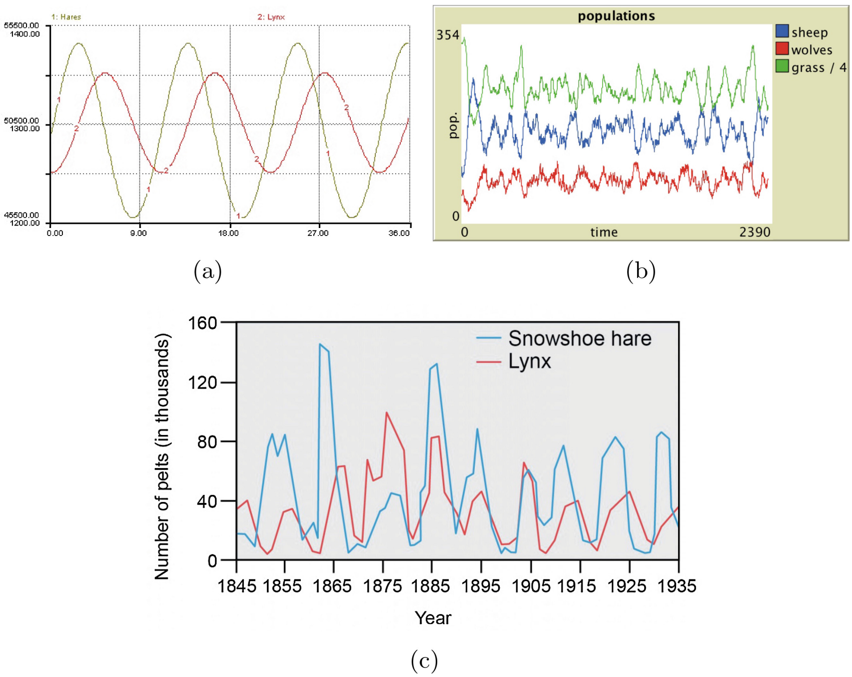


Fig. 1. Two models of predation compared to real world observations: (a) the Lokta-Volterra equational models [11, 19], (b) the Wilensky-Reisman multi-agent-based model (middle) [22], and (c) real world data from a lynx-hare population in Northern Canada [15].

equational models often require bigger changes or completely new equations even for small adjustments, (3) visualization of individual agents and their dynamics afford greater realism compared to graphs of populations [24]. These advantages make it possible for even high school students to easily learn topics that used to be hard for college graduates in related fields [22].

As Fig. 1 shows, a comparison between the real data, the equation-based model, and the multi-agent-based model shows that real world phenomena produce patterns that are more similar to the outcome of the multi-agent-based model. The outcome of the multi-agent-based model is similar to the equation-based model but with more noisy fluctuations, which the equation-based model shows less, because it is a discrete model. In this paper, we attempt a very similar restructuration of an evolutionary biology topic, which is historically studied through equational models, and re-examine it through multi-agent-based modeling.

3 Developing a Multi-agent-based Thought Experiment on the Evolution of Gamete Dimorphism

There are two main types of reproductive strategies employed by organisms: sexual reproduction and asexual reproduction [6]. The most prevalent sexual reproduction strategy is called gamete dimorphism or anisogamy. Many animal and plant species, including humans, are anisogamous: one mating type (males) provides half the chromosomes by producing small cells in large quantities (sperm) and the other mating type (females) provides half the chromosomes by producing much larger cells in much smaller numbers (egg). When two such cells, called gametes, belonging to opposite sexes fuse, a zygote is formed and this zygote gradually grows into an adult [3,14].

The evolution of anisogamy is a yet to be resolved topic in evolutionary biology and is the foundation of theories on gender differences and relations [4]. This starts with the very question of "why do sexes exist?" [4,16]. Given that asexual production (*parthenogenesis*) actually has some distinct advantages in terms of numerical advantage in progeny, many have wondered why sexual reproduction evolved in the first place [6]. It is also not known why anisogamy prevailed over other sexual reproduction strategies. For instance, there are some fungal species which reproduce through more than two mating types [10] or by producing gametes of equal size (isogamy) [14], but they are exceptions. In this paper, we attempt to address the latter question because the discussion on the evolution of anisogamy mostly revolves around the validity of the assumptions of theoretical models [16]. The equation-based methods used in these models make it harder for beginners to join the conversation and domain experts to manipulate the models for further analysis. We argue that a multi-agent-based thought experiment of anisogamy can afford domain experts the ability to easily plug new assumptions into an existing model while making it significantly easier for non-experts to learn about anisogamy [22]. In this section, we describe the process of developing one such thought experiment through reviewing the literature on anisogamy, determining model assumptions, defining agent rules and designing the user interface.

3.1 Literature Review

Evolutionary theories in general try to show how it is that a trait might be selected when there are many competing treats. In the case of reproductive strategies, there is no clear answer on why anisogamy is a more successful strategy over isogamy or multiple mating types. The most accepted theory on the evolution of gamete dimorphism is called “the Parker-Baker-Smith (PBS) model”. It lays out mathematical formulations to determine the conditions for the evolution of anisogamy through a *zygotic fitness function* and a *gametic fitness function*. The PBS model makes three simple but powerful assumptions [5,14]:

1. individuals of a marine ancestor population produce a range of gametes and the fusion between pairs of gametes is at random at sea
2. each adult has only a fixed biomass available for gamete production
3. there is some sort of relationship between zygote fitness and zygote size

It is important to caution that we are far from having a model that offers a universal explanation yet. Many of these theories, including the PBS model, are actively debated [16] and there are still many questions that remain unanswered [4]. The PBS theory of evolution is generally viewed as a foundational model but not the ultimate answer [6]. Both the assumptions and the formulations of the model are challenged by other theorists [4,16]. There are also many theories that build on the PBS model and attempt to offer more explanatory value (e.g., [7]).

3.2 The NetLogo Model of Gamete Dimorphism

We develop our multi-agent-based thought experiment of anisogamy in the NetLogo agent-based modeling environment [20] as it provides powerful tools to model emergent phenomena through a beginner friendly programming environment that allows writing open, easily readable code and a rich set of visualization options [17,21]. In the model [1] [1], adults of two mating types begin with producing middle-sized gametes at approximately the same rate (isogamy). Every time an adult produces new gametes, there is a chance of a small, random mutation in the gamete size strategy. These mutations introduce a competition among multiple reproductive strategies. In this section, we describe the model’s assumptions, agent rules and interface in detail.

[1] Source code of the NetLogo model of anisogamy is openly available through http://modelingcommons.org/browse/one_model/5007.

The Assumptions and the Agent Rules. Similar to the existing theories in the literature, our model builds on the following set of basic assumptions that we appropriated from the PBS model and its derivatives [3–5, 12–14, 16, 18]:

1. Adults have limited lifetimes.
2. Gamete production budget is fixed and the same for all adults.
3. Gametes have limited lifetimes, too, but much shorter than adults.
4. A zygote has to achieve a minimum mass to survive.
5. There are initially two isogamous mating types in the population.
6. The gamete size and the mating type traits are inherited as a bundle.
7. The chance of a zygote inheriting these traits from either gamete is equal.

Assumptions 2 and 4 directly correspond to the 2nd and 3rd assumptions of the PBS model (Sect. 3.1). We implement the 1st assumption of the PBS model by implementing a random walk algorithm in the model's code. We also implement a lifetime mechanism to simulate successive generations, although there is no mention of this in the PBS model or other equational models. Based on these assumptions, we define three agent types as *adults*, *gametes* and *zygotes* and define simple rules for each agent type.

Rule set for adults *(at each clock-tick)*:
1. turn around randomly and move one step forward.
2. with probability P produce gametes:
 - randomly pick the new gametes' size (m_t) through a normal distribution with *mean* = *my gamete size strategy* (m) and *standard deviation* = σ.
 - hatch *own mass* $(M)/m_t$ gametes of my mating-type and of the size m_t
3. decrease the remaining lifetime by 1, die if no lifetime left.

Rule set for gametes *(at each clock-tick)*:
1. turn around randomly and move one step forward.
2. fuse (form a zygote) if touching a gamete of the opposite sex:
 - inherit the total mass of myself and my mating partner.
 - randomly inherit the mating type and gamete size strategy as a package
3. decrease the remaining lifetime by 1, die if no lifetime left.

Rule set for zygotes *(at each clock-tick)*:
1. decrease the remaining incubation time by 1. if incubation time is 0:
 - if *own mass (M)* mass is greater than the survival threshold ($M \geq \delta$), turn into an adult.
 - if *own mass (M)* is less than the survival threshold ($M < \delta$), die.

Interface and Parameters. NetLogo's interface affords easy manipulation of the parameters of the model, and we can observe the changes in the system visually through the model's world and plots. The *world* is a graphical window which is not a mere visualization but an actual space where the agents follow the rules and interact with each other [21], seen as the central window shown in Fig. 2. The adults are represented by circles with black dots in them. An adult's color (blue or red) represents its mating type. The tiny arrow shaped agents are the gametes produced by adults. They, too, are either blue or red but vary in size depending on their parents' gamete size strategy. Lastly, the egg-shaped agents with lighter shades of red and blue are the zygotes formed by the fusion of two gametes.

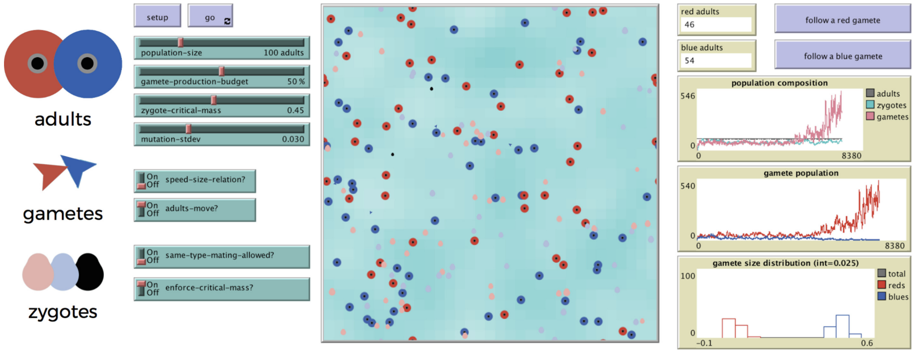
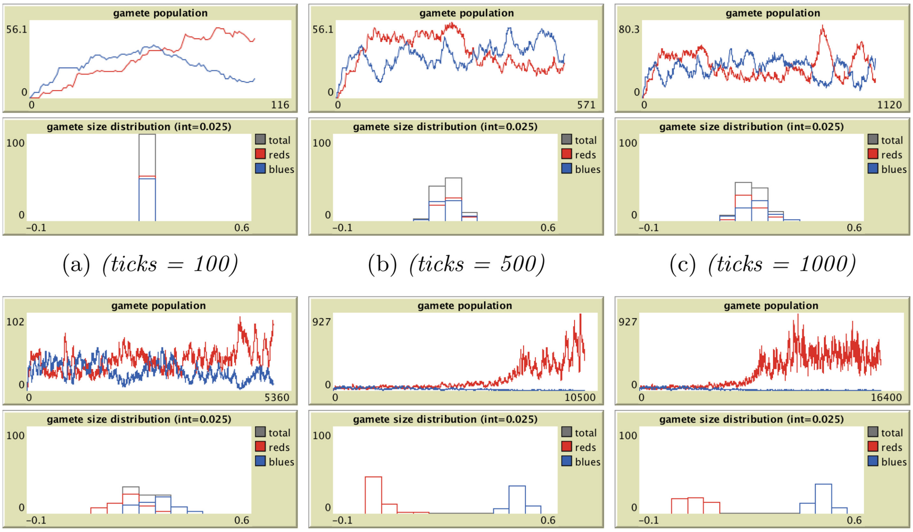


Fig. 2. The interface of the NetLogo Anisogamy model (Color figure online)

The first two plots on the right allow us to see the change in the overall population and the number of gametes of each mating type over time. The histogram on the bottom right shows the distribution of the gamete sizes at the observed clock-tick. The two integer outputs on the top right (blue adults and red adults) allow us to observe if the mating type balance is disrupted or not. The controls on the left allow us to change the parameters of the model so that we can test implicit and explicit assumptions. Each of these controls corresponds to bigger questions that we want to ask through this model. For example, one of the questions we want to ask is *"what, if any, thresholds of zygote critical mass effect the potential evolution of anisogamy"*, so we implement a *ZYGOTE-CRITICAL-MASS* slider that determines the threshold of mass that a zygote needs to achieve to survive. Similarly, we want to investigate whether the assumption of differentiation in mating types is viable, so we place the *SAME-TYPE-MATING-ALLOWED?* switch.

4 Findings and Discussion

A comparison of our multi-agent-based model and equation-based models of anisogamy highlights the advantages of multi-agent-based thought experiments. In this section, we first share the outcomes of our model with the default parameter-set, which corresponds to our basic set of assumptions (see Sect. 3.2). In this condition, we run the model with approximately 100 adults in a confined space. The average lifetime is 500 clock-ticks for adults and 50 clock-ticks for gametes. Because the model's space is 256 square unit-lengths and computing power is limited, we implement a carrying capacity mechanism. Whenever the model's adult population exceeds 100 members, some adults are randomly taken out of the population. This does not apply to gametes or zygotes. All adults are of 1 unit-length, mass of 1 unit-mass, and they move around randomly with the speed of 1 unit-length per clock-tick. Adults can use half of their mass for producing gametes. Initially, all adults have the same reproductive strategy of producing two middle sized gametes. Gametes move around randomly with the same speed, too, and they are only allowed to fuse with gametes of the opposite mating type. Lastly, the critical threshold for a zygote to survive is 0.45 unit-mass.



(a) *(ticks = 100)* (b) *(ticks = 500)* (c) *(ticks = 1000)*

(d) *(ticks = 5000)* (e) *(ticks = 10000)* (f) *(ticks = 15000)*

Fig. 3. The emergence of gamete dimorphism over time in the multi-agent model (Color figure online)

Figure 3 shows the outcome of a typical run with the default parameters. Each subfigure consists of two plots: a plot showing the change in the number of red versus blue gametes over time and a plot showing the distribution of gamete sizes at the presented clock-tick. Gametes of the two mating-types are represented with red and blue colored lines and bars in the graphs. As our model assumes that the reproduction budget is fixed for all the adults, a large gamete number means smaller gamete size, and vice versa. Figure 3a is a snapshot of the model after 100 clock-ticks and the subsequent subfigures are after 500, 1000, 5000, 10000 and 15000 clock-ticks. In our model, 15000 clock-ticks correspond to approximately 300 generations. This might be extremely small for such an evolutionary process in real life but in the small world of our thought experiment, it is enough to observe meaningful and consistent results.

As the first four subfigures show, the model starts with oscillations between two similar strategies. In this specific run, a stochastic disruptive event happens at about 7000 clock-ticks (Fig. 3e) resulting in one mating type getting committed to producing big gametes and the other to producing small gametes. In other words, anisogamy evolves and is sustained. Figure 4 presents the results of 300 runs with this default parameter-set over 20000 clock-ticks . Each data point presents the average number of red or blue gametes in the last 5000 clock-ticks, which provides more reliable data because the number of gametes in the model oscillates continuously. We clearly observe evolution of two distinct gamete size strategies at the end of each simulation run (Fig. 4). Statistical analysis of this data shows that there was a significant difference between the number of large gametes ($m = 1.735, sd = 0.184$) and the number of small gametes ($m = 437.675, sd = 19.505$); $t(299) = -384.221, p < 0.0005$. These findings provide a theoretical explanation of not only why but also how anisogamy might have evolved, as well as supporting previous theory on the instability of isogamy in the long run [18].

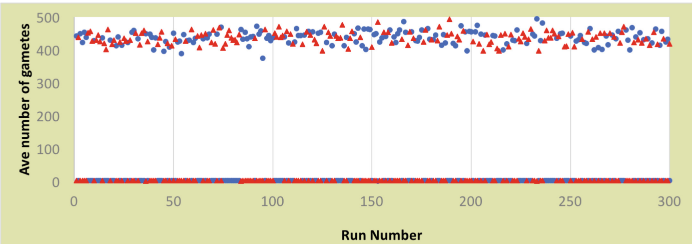
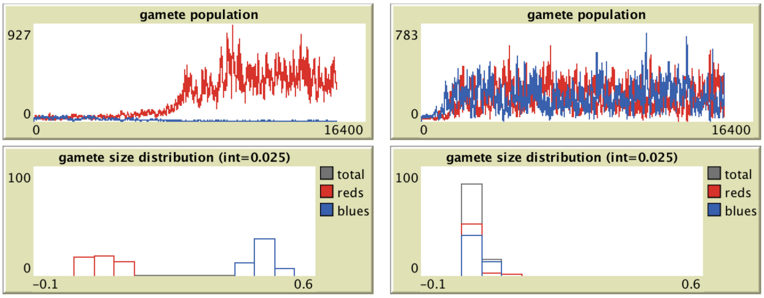


Fig. 4. Testing the model with default parameters (n = 300, ticks = 20000).

The affordances of multi-agent-based thought experiments become even more noticeable when it comes to testing assumptions of a model to answer *"what if?"* questions. In the following sections, we test an explicit and an implicit assumption of the PBS model, as well as another non-PBS assumption that is common in the literature. We not only show the ease of doing this through our model but also demonstrate how powerful the outcomes of such assumption tests can be.

4.1 Zygote Survival as a Function of Zygote Mass

We begin testing assumptions with one of the main assumptions of the PBS model concerning the relationship between viability of a zygote to its size [3,5,14]. We call this the ZYGOTE-CRITICAL-MASS assumption, which can be turned on and off easily with a switch on the models interface (see Fig. 2). With the default parameter-set of the model, we observe the emergence of anisogamy after 10000 ticks. We keep all the other parameters the same, but allow zygotes to survive regardless of their mass and run the model again. As seen in Fig. 5b, the gamete sizes and gamete population for both sexes fluctuate over time with the overall direction of reduction in the size. Anisogamy does not evolve when each zygote survives regardless of its mass.



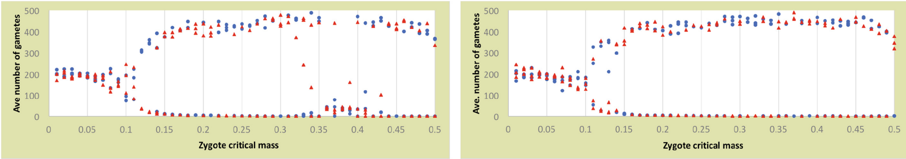
(a) *critical mass enforced* (b) *critical mass not enforced*

Fig. 5. The comparison of the model outcomes with ENFORCE-CRITICAL-MASS? switch turned on and off. (Color figure online)

We also conducted an experiment running the model starting with 0.0 as the value of the ZYGOTE-CRITICAL-MASS variable and then incrementing it by 0.01 until 0.5 over 20000 ticks. For each value, we ran the model 3 times, so we ended up with a total of 150 experiments. Figure 6a shows the results of this experiment. Once again, each data point corresponds to the running average of the number of gametes in the last 5000 ticks of each run. The most important outcome of this test is the fact that anisogamy did not evolve and isogamy was sustained when the value of the ZYGOTE-CRITICAL-MASS parameter was below 0.1, which is consistent with the assumptions of the PBS model [5,14]. Surprisingly, we also noticed some runs which did not result in anisogamy between the range of 0.3 and 0.45. We hypothesized that anisogamy would still evolve in this parameter space in a longer experiment. Accordingly, we conducted the same experiment but this time over 200000 clock-ticks and the results confirmed our hypothesis (Fig. 6). Once again, these findings align with the PBS model's assumption that *for anisogamy to evolve, some sort of a relationship between the zygote size and zygote survival is necessary* [6,14].

4.2 Mating Types

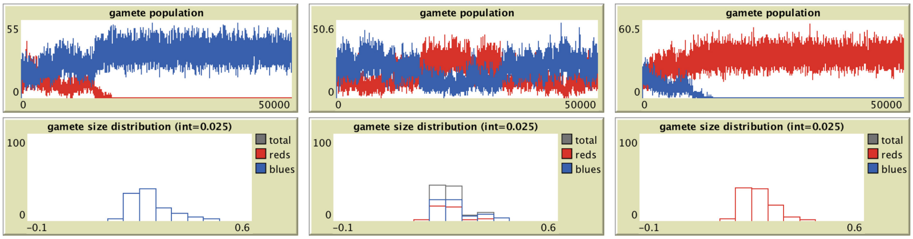
Another affordance of multi-agent-based thought experiments is the possibility of testing implicit assumptions. For instance, the existence of two mating types is a common assumption in many models of anisogamy, but it is rarely discussed explicitly (e.g., [5]). Our model assumes two mating types, too, but it is actually possible to test this assumption indirectly by allowing gametes of the same mating type to fuse. When we run the model with this alternative



(a) *(ticks = 20000)* (b) *(ticks = 200000)*

Fig. 6. Testing the model with a range of ZYGOTE-CRITICAL-MASS values between 0 and 0.5 (n = 150).

assumption, we observe that anisogamy does not evolve. Instead, there are two possible outcomes. In most of the runs, genetic drift [8] happens and one mating type prevails over the other (Figs. 7a and c). However, in some rare occasions, we observe almost no quantitative change in the population composition (Fig. 7b) because, by random chance, it takes more time for genetic drift to emerge in some runs (as in Sect. 4.1). These results provide support for the implicit assumption that mating types are required for anisogamy to evolve. On the other hand, our model currently does not allow testing the possibility of more than two mating types. This could be an interesting follow up on our test, and it is possible to do it with a few changes in the model's code.



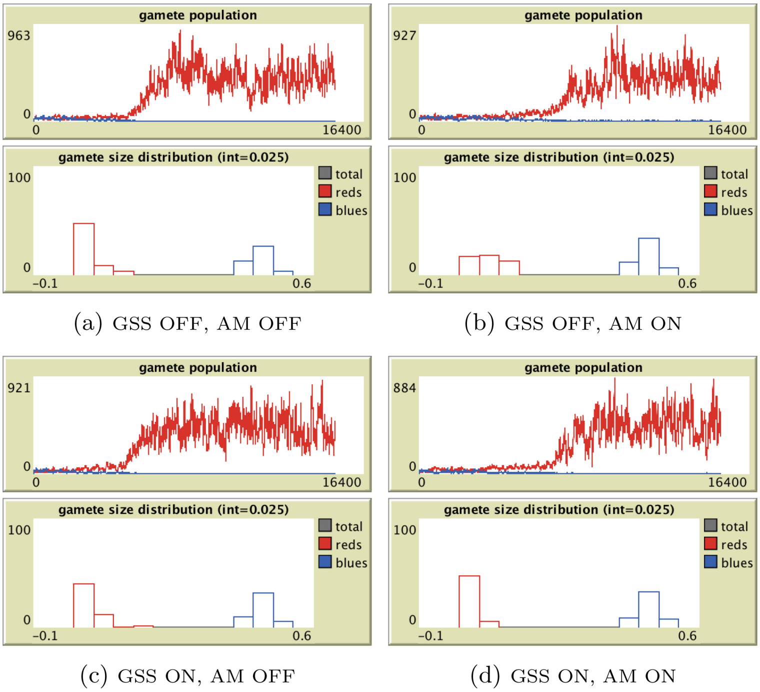
(a) run number 1 (b) run number 2 (c) run number 3

Fig. 7. The outcome of the model when fusion between two gametes of the same mating type is allowed *(ticks = 50000)* (Color figure online)

4.3 Adult and Gamete Motility

Another debated topic in models of anisogamy is the role of gamete and/or adult motility in the marine environment [4,16]. Some of the models assume that the speed of a gamete is inversely related to its mass according to Stokes Law [7], while others challenge the validity of this assumption [16]. As the actual physics of locomotion in water is somewhat complex, our point is to test whether a relationship of this sort is needed for the evolution of anisogamy.

Our model allows us to (1) make all the gametes move with the same speed or *with a variable speed that is inversely related to a gamete's size*, and (2) make



(a) GSS OFF, AM OFF (b) GSS OFF, AM ON

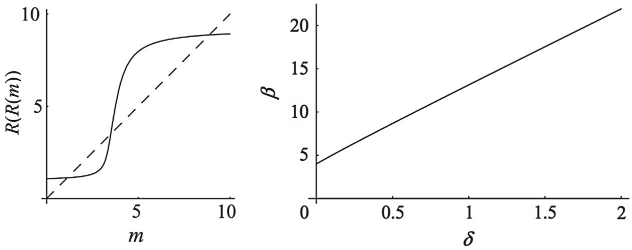
(c) GSS ON, AM OFF (d) GSS ON, AM ON

Fig. 8. The outcomes of the model when gamete-speed size relation (GSS) and adult motility (AM) assumptions are tested *(ticks = 15000)* (Color figure online)

adults move around randomly with the same speed or *remain stationary* (see Sect. 3.2). In our runs with the default parameter-set, the adults were moving and gamete size had no relationship with gamete speed. We tested the model by varying these parameters but to our surprise, we did not observe any significant differences in the model's outcome (Fig. 8). This finding directly contradicts some studies in the literature that claim that gamete motility is a critical factor in the evolution of anisogamy (e.g., [7,13]).

4.4 A Qualitative Comparison Between the Two Models of Anisogamy

In this section, we present a "relational alignment" [2,23] between our multi-agent-based model and the equational PBS model developed by Bulmer and Parker by qualitatively comparing the relationships between critical parameters of these two models and the evolution of anisogamy as a continuously stable strategy (ESS [12]). These critical parameters are gamete size (m), zygote size (S), and parameters that determine viability of gametes (α) and zygotes (β). Figure 9 shows two plots from Bulmer and Parker's mathematical formulation of the PBS model. Figure 9a is concerned with the conditions that result with anisogamy as ESS and Fig. 9b is concerned with a critical threshold for zygote survival in an anisogamous ESS [5].



(a) (b)

Fig. 9. Plots from Bulmer and Parker's equational PBS model of anisogamy: (a) anisogamy as ESS for given m and β values and (b) the critical value of β above which anisogamy evolves as a function of δ [5].

Bulmer and Parker use the PBS model to explore the parameter space for the parameters β and δ to find a parameter range over which anisogamy would evolve as an evolutionary stable strategy (Fig. 9b). β is a parameter that determines the shape of the response strategy function and δ is a parameter related to the gamete critical mass. In our multi-agent model of evolution of anisogamy, we demonstrate that anisogamy evolves as an ESS as reliably over the default parameter range (Fig. 4). We have also demonstrated that our multi-agent-modeling approach to evolution of anisogamy using NetLogo as a modeling environment allows as such comparison where we have investigated the parameter range for zygote-critical-mass (Fig. 6). Hence, these two models are qualitatively similar, or relationally aligned, in terms of inputs (conditions) and outputs (evolution of anisogamy as an ESS).

5 Conclusions

We argued that multi-agent-based models can be used to express scientific domain knowledge in the form of thought experiments. As a case study, we developed a multi-agent-based thought experiment on the evolution of anisogamy, which is the phenomenon of male species producing numerous small sperm cells and female species producing only a handful of large egg cells for reproductive purposes. We noted that anisogamy is a topic in evolutionary biology with direct implications on the evolution of animal and plant species, but it is yet to be resolved. We reviewed the evolutionary biology literature and developed a model in the NetLogo agent-based modeling environment building on a set of assumptions that we adopted from previously research.

Our model provided similar results to the equation-based models of anisogamy but allowed us to easily test explicit and implicit assumptions suggested by previously offered theories. For example, we were able to confirm that the existence of two mating types is a necessary prerequisite for anisogamy to emerge, and we showed why anisogamy does not evolve when any two gametes can fuse with each other [5,14]. On the other hand, we found no evidence of a possible relationship between adult or gamete speeds with the evolution of anisogamy [7,13].

Our study demonstrates that multi-agent-based thought experiments can allow scientists and theorists to explore a wide range of subtle and difficult *"what if"* questions. One can think of a new question and almost immediately manipulate the model to answer it. Even a strong mathematician may not be comfortable changing the equation-based models of anisogamy, but making changes in our multi-agent-based model of anisogamy is almost *mind-to-fingers*. More importantly, our model provides such opportunities not only to scientists but also to informed citizens and younger students without having to master all the formal mathematics. We argue that such multi-agent-based restructurations would make scientific domain knowledge more accessible for a wider population and speed up the progress in currently unresolved topics like the evolution of anisogamy.

5.1 Limitations

It is important to note that the outcomes of our model are by no means definitive as it is the case for all the other theoretical and equational models in the literature [4,6]. Because our goal was to primarily demonstrate the advantages of multi-agent-based thought experiments, we left out some theoretical considerations in this paper such as the possibility of more than two mating types existing in the population or a more comprehensive comparison between our model and the PBS model [5,14]. In future studies, we hope to focus, in greater depth, on the theoretical implications of our model for the field of evolutionary biology. We also hope to conduct research which explores the use of this multi-agent-based thought experiment and similar approaches in educational settings.

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