5-2020

Emergent Seedling Spatial Patterns Following Insect Seed Predation in a Simulated Population

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EMERGENT SEEDLING SPATIAL PATTERNS FOLLOWING INSECT SEED PREDATION IN A SIMULATED POPULATION

by

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Thesis submitted in partial fulfillment of the requirements for the degree

of

DEPARTMENTAL HONORS

in

Biological Science in the Department of Biology

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Spring 2020

ABSTRACT

Tropical vertebrate species have faced increasing pressures from hunters, causing many to become locally extinct. I used an agent-based model (NEDD) to investigate the influence of dispersal and insect seed predation on seedling survival. Statistical dispersal kernels were used to simulate the dispersal of seeds. The NEDD model generates survival and spatial data from parameter sets, which were chosen based on a Latin-Hypercube experimental design. Spatial point analysis was performed on the output data to identify trends in spatial clustering patterns as the parameter space was changed. The results of this investigation suggest that there is a positive association between the proportion of seeds that are distributed at a frugivore site and the successful recruitment of seeds. Increasing frequency of frugivore sites was shown to have a negative impact on seedling recruitment. Understanding the role of tropical vertebrates in mediating seed dispersal and survival may inform management decisions in the near future.

ACKNOWLEDGMENTS

I would like to acknowledge Dr. Noelle Beckman for guiding me and supporting me through three years of research. Her encouragement throughout my undergraduate career was the spark that ignited my passions for ecology, programming, and science communication. She is an exceptional mentor. I would also like to thank the brilliant members of the Beckman lab for being excellent friends and dependable collaborators. A final thank you goes out to my friend Dr. Will Pearse for his ceaseless charisma and his endless enthusiasm. Thank you.

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INTRODUCTION

A large proportion of human activities have negative impacts on native fauna and flora. One of the obvious ways that local communities put pressure on native populations is by killing or capturing native animals. The effect of removal of animals on the native populations has become more apparent in recent years, resulting in local and global extinctions of vertebrate species (Hoffman 2010, 2011). However, it is less obvious how large-scale losses of vertebrate seed dispersers are impacting non-target species, such as plants and invertebrates. Forests that are depleted of animals appear to be otherwise intact for a number of years; this phenomenon is called “empty forests” (Redford 1992, Wilkie et. al. 2011).

Despite appearances, empty forests are suffering from disruptions to ecological processes (Hoffman 2010, 2011). Frugivorous vertebrate populations are key to the health of forested populations because they disperse seeds throughout the forest. Active seed dispersing populations are key to maintaining the extreme biodiversity of tropical ecosystems and the genetic diversity of the fauna that grow within them (Vellend 2010, Kremer 2012). High levels of genetic and species diversity are a crucial resource for ecosystems because they allow for the ecosystems to be resilient in the face of global changes (Travis et. al. 2013).

While the removal of vertebrate seed dispersers impacts many areas around the world, the decline of vertebrate dispersers has become particularly evident in tropical regions (Hoffman 2010, 2011). More than 80% of trees in these regions are dependent upon vertebrates to disperse their seeds (Howe and Smallwood 1982). These seeds are commonly dispersed when frugivores defecate seeds from fruit which they previously collected and consumed. Studies focused on understanding the changes in composition of forests experiencing defaunation have suggested that depleted forests become more dominated by the plants that specialize in dispersal mechanisms that make use of non-game species or abiotic dispersal modes (Terborgh et al, 2008; Effiom et al, 2013; Wright et al 2007). Further empirical studies have suggested that reductions in

frugivore populations reduce overall seed recruitment (Harrison et al, 2013), reduce the distance between the recruited seeds and the parent tree (Babweetera and Brown, 2010), and reduce local species diversity (Nunez-Iturri and Howe, 2007).

The removal of seed dispersing vertebrates from wild areas is a problem that faces the globe. As of 2013, 25.9% of all seed dispersing vertebrates face the threat of extinction (Aslan, 2013). The large scale of defaunation combined with the long generation times of many trees raises the concern that there are latent effects of species extinctions that have yet to be revealed (Brodie et al, 2009). Understanding the dispersal mechanisms underlying biodiversity may supply information about what species are critical to preserving biodiversity in species-rich forests. This information could direct conservation efforts towards key species thereby maximizing return on investments.

Preparing strategies for managing Earth's forests in the face of a changing global environment demands that we understand how defaunation is going to alter the composition and resilience of the world's forests. In advancing the study of defaunation, computer simulations have been used to model how seed dispersers and seed predators interact to create patterns of recruitment that sustain biodiversity (Adler and Muller-Landau, 2005; Muller-Landau and Adler, 2007). Simulated environments and analytical mathematical models are important to the study of defaunation because they produce results much faster than traditional empirical data sets. Studying defaunation using empirical data sets presents barriers to research because tree populations must be studied over long periods of time and defaunation occurs at large scales. The long generation time of many trees also means that the full effect of rapid defaunation won't become apparent in empirical data sets until a lengthy latency period has passed.

This investigation uses an agent-based model developed by Dr. Beckman and Dr. Adler to examine how interactions between female insect predators and vertebrate seed dispersers affect the overall success of recruitment. The parameter space of each variable was sampled using a Latin-Hypercube experimental design, culminating in a total of 300 simulations.

METHODS

This study investigates how the behaviors of vertebrate seed dispersers and insect seed predators influence the successful recruitment of seeds. Results from this study were generated by varying the inputs to a simulation which models the interactions between seeds, vertebrates, and insect seed predators. The simulated environment is an example of an agent-based model. It was developed by Dr. Beckman (Utah State University) and Dr. Adler (University of Utah) as a non-invasive method of investigating the impacts of seed dispersal in areas with high biodiversity. The output of the NEDD code environment classifies seeds as either "success" or "fail." The successful seeds were not consumed by insect seed predators. As such, they have the potential to successfully recruit into an adult tree.

Abundance Parameters

The NEDD simulation environment has 20 input parameters which can be varied either continuously or discretely. These parameters are of three basic types. The first class of parameters are focused on the abundance of each agent within the model. The model includes reproductive adult trees, female insect seed predators, frugivore sites (locations where social animals congregate), and seeds. The NEDD simulation environment encompasses a 9 ha (300 x 300m) area, so our experiment samples the parameter space for the frequency of each agent within a value range that represents reasonable densities.

Mean Parameters for Dispersal Kernels

A second class of parameters contains inputs for the statistical functions that act as dispersal kernels. Source trees and frugivore sites are randomly populated into a two-dimensional grid. Seeds and insect seed predators are then dispersed around frugivore sites and reproductive adult trees. Seeds may be dispersed from source trees by gravity, or they may be dispersed from trees by vertebrate seed dispersers which drop the seeds in-transit from the tree. Gravity dispersal is modeled using a Gaussian kernel with a mean value of 5 meters. The mean value for the

gravity dispersal kernel is kept constant among all simulations performed. In-transit seed dispersal processes are modeled using a two-Dimensional *t*-distribution (2Dt). The mean value for the in-transit seed dispersal (kmmean) ranges from 5 to 160 meters. Insect seed predators are only dispersed from reproductive adult trees. A 2Dt kernel with a mean dispersal distance (rhomean) ranging between 5 and 160 meters is used to model dispersal of insect seed predators from adult reproductive trees. In addition to being dispersed from adult reproductive trees, seeds are dispersed from frugivore sites. These are sites where social vertebrate seed dispersers congregate. Examples of seed dispersers that congregate socially include rhinoceros, tapirs, primates, and bats. These sites serve as latrines, resting sites, and fruit-processing sites for vertebrate seed dispersers. A key parameter within this model provides a proportion (p_s) that dictates how many seeds are dispersed by frugivores at the frugivore sites as opposed to being dispersed in-transit.

Foraging Behavior Parameters

A third class of parameters define the foraging behavior of female insect predators. These parameters together define the probability that a seed will survive given that it is within a certain distance (det.rad) of an insect seed predator. Each simulation sets a value which defines the shape (det.func) of an insect seed predator's search function. Additionally, the time a beetle spends handling seeds they find (th) and the speed with which they detect seeds (sd) are incorporated into their simulated foraging behavior by using a modified Holling's Disk Equation (Holling 1959). The equation of the probability of seed survival was developed by Drs. Beckman and Adler.

Sampling Parameter Space

We used the NEDD environment to process a total of 300 simulations. Before performing the simulations, the parameter space of each simulation input was narrowed to ranges that reflected realistic minimum and maximum values. The values for each simulation were

subsequently sampled according to the Latin-Hypercube sampling procedure. Using this process, we defined unique combinations of agent abundance, seed dispersal, and predator foraging behavior for each of 300 simulations. The NEDD environmental simulations output reported the status of seeds at the end of the simulation as either a “success” or a “fail.” Success indicated that the seed evaded the beetles and survived after one time step. Having evaded insect predators, these seeds have the potential to recruit into reproductive adults.

Binary Logistic Regression Analysis

Successful predator evasion was modeled by creating a binary logistic regression model which made use of 13 of the 20 parameters that were sampled. Only continuous parameters were used in the creation of our binary logistic model. This was facilitated by the glm() package in R (R Core Team, 2020). The goodness-of-fit of the model was evaluated by calculating McFadden’s Pseudo R^2 (McFadden 1977). The Pseudo R^2 is calculated by subtracting the quotient of the log likelihood of the current model over the log likelihood of the null model from 1 (See Equation 1).

Equation 1: McFadden's Pseudo R Squared

$$R^2_{McFadden} = 1 - \left(\frac{\log(L_c)}{\log(L_{null})} \right)$$

where...	$\log(L_c)$	is the fitted model
	$\log(L_{null})$	is the null model

Equation 1: How to calculate McFadden's Pseudo R-Squared

After calculating goodness-of-fit, the model coefficients were analyzed to determine the effect sizes for each parameter (Table 1). The link function used for binary logistic models converts probability to the log of the odds of success. This procedure eliminates the range problem inherent to working with binary data. As a result, the coefficients (effect sizes) report the

effect that increasing a parameter by one unit has on the log of the odds of a seedling being successful. Although the coefficients generated by our binary logistic model all give the effect size per 1 unit change, the units differ between parameters. The effect sizes for means of dispersal kernels were compared against each other because their units represent standardized distances in the NEDD environment. All simulations and analysis for this study were performed in R version 3.6.3 (R Core Team, 2020).

RESULTS

Goodness of Fit

The goodness-of-fit of the binary logistic regression model was evaluated using McFadden's Pseudo $R^{2,}$, which produced a value of R^2=0.045. This result indicates that the binary logistic model that we created from the continuous variables poorly predicts seedling success. Unlike other forms of linear regression, it is expected that the $R^{2,}$ value of a binary logistic regression will be small. McFadden suggests that values as low as 0.2 represent an excellent fit (1977). We conclude that the generated model is a poor predictor of seedling success. We suggest that non-parameter attributes of the data be evaluated to determine if the spatial arrangement of seeds relative to either con-specific adults or frugivore sites are better predictors of seedling success. The relatively poor ability of these parameters to predict seedling success may be an artifact of multicollinearity among the independent variables.

Significance

Although the binary logistic regression model is poorly fit to the survivorship data, the output of the model is still useful for evaluating data trends. The binary logistic regression model revealed that all of the continuous parameters in the model were significant at the significance level of α=0.001.

Model Trends

The model reported that increases in tree abundance (nadult), proportion of dispersed seeds distributed to vertebrate sites (p_s), mean displacement of seeds distributed around frugivore sites (k0mean), abundance of insect seed predators (nb), insect speed/detection (sd), probability of a seed being found by a disperser (q_seed), mean dispersal distance for in-transit seeds (kmmean), and handling time for seed predators (th) increased the log-odds of seeds escaping mortality caused by insect seed predators. The model reported that increases in the mean dispersal distance for seed predators (rhomean), the insect search radius (det.rad), the shape

parameter for the insect's search function (det.func), the abundance of frugivore sites (ss), and the beetle departure rate (delta0) reduced the log-odds of seeds escaping mortality caused by insect seed predators.

Comparison of Dispersal Kernel Means

The model reports that the effect size for increases in the mean dispersal distance of seeds dispersed from frugivore sites (3.90e-04) is larger than the effect size for increases in the mean dispersal distance of seeds dispersed from reproductive adult trees (2.39e-02). Increasing the average distance of seeds from frugivore sites increased the log-odds of seeds escaping insect-driven mortality 61 times better than increasing the average distance of seeds from con-specific reproductive adults. The effect size for the mean dispersal distance of insect seed predators (-4.07e-3) had a magnitude of effect that was intermediate to the dispersal kernels for seeds.

Comparison of Sleeping Sites and Reproductive Adults

A comparison between the effect size of increasing the abundance of reproductive adult trees (3.23e-03) and the abundance of sleeping sites (-1.02e-2) suggest that increasing the number of reproductive adult trees increases the log-odds of seedling success faster than increasing the number of frugivore sites. The effect size for increasing the proportion of seeds distributed by vertebrates at frugivore sites (rather than in-transit) was the largest reported effect size in the binary logistic model (0.443). This suggests that seeds are more likely to survive at frugivore sites than around reproductive con-specific sites.

Table 1: Effect Sizes

Parameter	Effect Size	Description
(Intercept)	−1.58e+00	
nadult	3.23e−03	Tree Abundance
p_s	4.43e−01	Proportion of dispersed seeds distributed to frugivore sites
rhomean	−4.07e−03	Mean dispersal distance for insects
det.rad	−1.26e−01	Half of an insect's search radius
dep.func	−4.26e−02	Shape parameter for an insect's search function
ss	−1.02e−02	Sleeping Site Abundance
k0mean	2.39e−02	Mean displacement of seeds distributed around frugivore sites
nb	2.66e−06	Abundance of insect predators
sd	7.43e−03	Insect speed * detection width in ground (m^2/hr)
q_seed	5.78e−02	Probability a seed is found by a disperser
kmmean	3.90e−04	Mean dispispersal distance for in−transit seeds
th	8.24e−02	Handling time for seed predators
delta0	−1.08e−02	Insect departure rate with one seed in disk (1/hr)

** Effect sizes are reported as the log of the odds of successful seed recruitment.

Table 1: The size of the coefficients produced by a binary logistic regression model performed for the continuous parameters present in the NEDD code simulation.

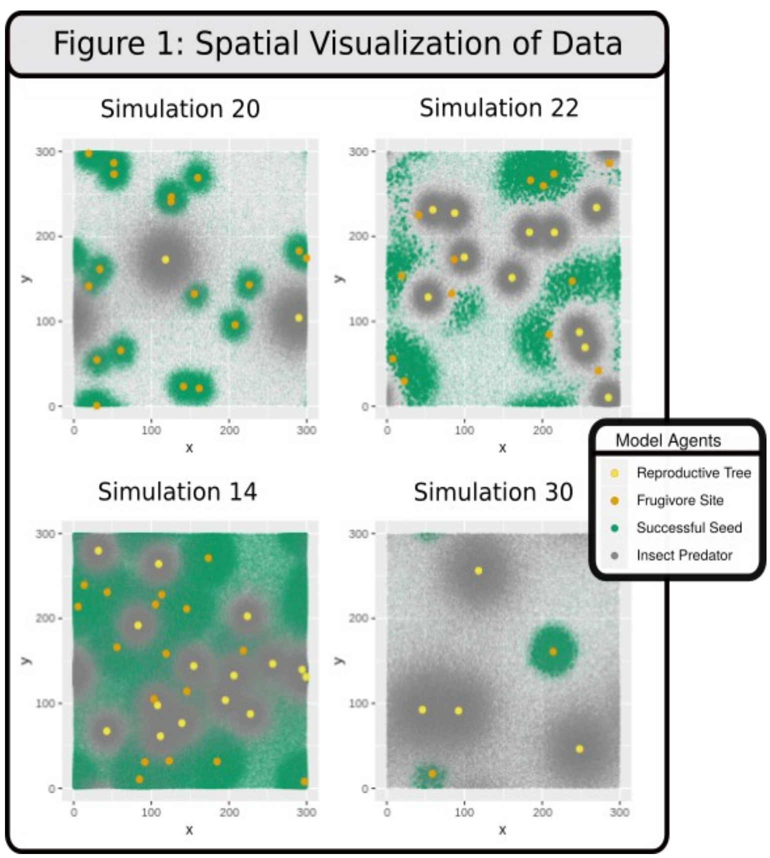

Figure 1: Visualization performed as part of this investigation

DISCUSSION

Binary Logistic Regression

The McFadden's Pseudo R^2 calculated from our regression model indicated that the model was poorly fit to the data for seedling success. The experiment we performed was meant to simulate an environment that contains both stochasticity and complexity. Therefore, it is no surprise that the logistic regression model was not able to identify a clear threshold for seedling success. Analyzing the effects of increasing the mean dispersal distance of seeds gives insight into why vertebrate seed dispersal is important to the successful recruitment of trees. This study indicated that the success of seeds increased as vertebrates became more active in the simulated environment. However, a better Pseudo R^2 might be found by using the relative position of agents as a parameter in a new model. Incorporating the proximity between a frugivore site and its nearest source tree may add crucial information about the relative positions of NEDD agents that is not available by analyzing mean dispersal distances alone.

Dispersal Kernels

We anticipated that increasing the means for dispersal distance of seeds would increase the log-odds of seedling success. We also expected that increasing the dispersal distance of insect seed predators would increase the log-odds of seeds getting eaten by insects. In this set of simulations, the vertebrate seed dispersal was limited to two types. Animals either dispersed seeds around the source tree or at their frugivore sites. It has been proposed that highly mobile vertebrate seed dispersers place seeds across their entire habitat. This feature has been incorporated as an optional component of the NEDD environment in the form of a dispersal kernel that disperses seeds in a random uniform pattern across the simulated environment. Future studies may focus on indicating how including this additional method of seed dispersal alters the effect size of each of the dispersal kernels seen in this study. Such an investigation would give

insight into the role that highly mobile seed disperser play in maintaining biodiversity.

Measures of Abundance

The model reported that increasing the number of adult reproductive trees increased the log-odds of seedling success in the area. This result was anticipated because simulations with more trees produce more seeds, which gives them more opportunities to successfully recruit. The NEDD environment only models whether or not a seedling escapes predator-driven mortality. Therefore, the positive impact of increasing the density of con-specific trees does not account for the negative effect that intraspecific competition has on successful seedling recruitment.

The logistic regression model also reported that increasing the number of frugivore sites decreased the log-odds of seedling success in the area. Even though the density of frugivore sites increases, the total number of seeds being dispersed remains the same. Therefore, this result may indicate that adding frugivore sites has the effect of reducing the maximum density of seeds in any given area. Reducing seedling density may also reduce benefits that seeds get by satiating predators. Consider a case where a predator can detect and prey on 2 seeds per 10 square meters. If an area contains two insect predators and 15 seeds, then 4 of those seeds will satiate the predators and 11 of the seeds will survive. The negative effect of frugivore sites on seedling success which was reported by the model may be indicating that removing seeds from high density areas reduces benefits accrued by satiating insect predators. While the effect size of this parameter suggests that seeds were less likely to survive in general, the effect size for increasing the proportion of seeds dispersed at frugivore sites suggests that frugivore sites have a positive effect on the log-odds of successfully evading predator-driven mortality. This indicates that seeds dispersed from frugivore sites tend to be more successful than seeds dispersed from source trees.

Increases to the density of the insect predator population had a small positive effect on the log-odds of seed success. The absolute effect size of increasing the insect predator population is the smallest effect size present in the regression output (2.66e-06). However, the relative impact

of increasing the number of insect predators actually has a larger positive effect on seedling success than some other variables because there is a large potential for the number of insects to fluctuate. The simulations tested in the NEDD environment sampled the parameter space for insect abundance in the range of 1,000 to 100,000 insects. Therefore, the insect abundance has the potential to increase the log-odds of survival by 2.66e-03. This doesn't create as much positive impact on seedling success as adding several reproductive adult trees. However, this does represent a substantial positive effect of increasing the size of the beetle population. This phenomenon remains unexplained, providing fertile ground for assessment with more advanced spatial and statistical analysis.

Foraging Behavior

The regression model reported that seedlings were more successful when insects searched smaller areas and spent more time handling the seeds that they detected. Seeds also benefited in simulations where insects had slower departure rates. Surprisingly, the model also reports that the seeds benefited in simulations where the beetles had a higher value for the speed detection by area parameter. These results generally communicate that seedlings benefit from having insect predators that are not well suited to find them and spend long period of time handling each seed that they do find.

Future Directions

Future analysis of this model should incorporate spatial analysis which accounts for the relative positions of each of the agents in the model. Several surprising results were produced by this simulation. Specifically, we did not expect to see positive effects for increasing the number of insect predators and negative effects for increasing the number of sleeping sites. Additional investigations should seek to understand the mechanisms that underlie these phenomena.

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AUTHOR BIOGRAPHY

Justin Tirrell graduated cum laude from Utah State University in the Spring of 2020 with a degree in Biology, minors in Philosophy and Chemistry, an undergraduate researcher designation, and Departmental Honors. During his time at Utah State University (USU), he engaged in the study of Ethics, participating in intra- and inter-collegiate Ethics Bowl competitions for his region. While at USU, Justin enjoyed participating in book clubs hosted through the Honors Department and through the Society for the Advancement of Ethical Leadership (SAEL).

After taking a year long leave of absence, Justin embedded himself in the Ecology research community at USU. His enthusiasm for technology grew as he began attending coding competitions, hack-a-thons, monthly meetings for the local DefCon (435) group, and weekly meetings as part of the USU Biological Nerd Herd. In particular, Justin enjoyed engaging with the community as a volunteer. While a student, he spent time volunteering as a friend at the Kid's Place, as a volunteer note-taker for the Disability Resource Center, and as the Head of Professional Development for the USU Science Council.

Justin's research allowed him to engage with regional and international investigators in answering scientific questions about biodiversity. He collaborated with USU professors to perform both greenhouse experiments and field experiments, and he supported fellow students as an Undergraduate Teaching Fellow. After 3 years of engagement with research, Justin has cultivated a passion for engaging in conservation, research, and open source communities.

REFLECTIVE WRITING

After my second year at Utah State University (USU), I left my education to accept a job in Alaska with some friends. During the following year, I explored many beautiful places in America. I explored in Denali National Park. I solo-backpacked in Idaho's wilderness. I hiked portions of the Pacific Coast Trail and the Appalachian Trail. I baked in Georgia's summer sun, and I froze in Michigan's lake weather. When I returned to USU a year later, I felt that I had formed a connection to America's natural resources. I remember staring at the forests which drape the mountains around my home and wanting to understand how they moved and changed through time. I studied mushrooms, sketched flora and fauna, and fearlessly adventured with tireless friends. My capstone project—which investigates how insect seed predators and vertebrate seed dispersers shape the dynamics of forests—reflects the sense of fascination for nature that I felt and the efforts I have made to understand the dynamic processes that change our world.

Through the last 3 years, I have been an active member of the Beckman Research Lab. Being part of the Beckman Lab has opened many doors for me, and I have grown substantially as a researcher while volunteering and working within the lab. Three years ago, I asked Dr. Beckman to allow me to join her lab because I wanted to use mathematical and computational models to describe biological populations. The completion of this capstone project is evidence that I have come a long way towards achieving that goal. All of this progress has been made possible because I have had amazing mentors. During the Spring of 2019, I submitted proposals for the URCO grant and the Peak Fellowship opportunity. I remember being nervous about the application and seeking guidance from my friend Dr. Pearse. It was that day that I came to realize that I had the full support of my mentors. In the words of a friend: they had my back. Soon after that conversation, I asked myself what would be the best way of thanking people who invest in me. My answer is that the only genuine thank you that I can give someone who invests in my

potential is to realize that potential. As such, I have viewed this capstone project as my way of expressing gratitude towards Dr. Beckman, Dr. Pearse, and the friends and family that have encouraged and supported me.

As a Biology student, in-depth statistics and computer science were not a part of my standard curriculum. However, they quickly became a staple to my work as a researcher. For the last 3 years, I have been on a journey in which I have learned about open source software and embedded technology. My research pushed me to discover communities that develop R packages and share them freely with the community. Engaging with open source materials has showed me that there are communities of people who volunteer their efforts, time, and resources for the sake of making the world a little bit better. I am inspired by these open source communities because their efforts have produced tools that facilitate my research, my efforts in science communication, and the way that I organize my life! As a result, I am committed to contributing to these communities by using my qualifications as a biological researcher. I have begun to realize this commitment by collaborating with conservationists across the globe to assist with the development of tracking systems to be used in disrupting illegal wildlife trafficking.

Pursuing this capstone project was a significant and worthwhile investment. It has given me the opportunity to be a part of a large-scale mathematical biology investigation. When this study has been completed, I will be a published author in the field of mathematical ecology. This publication will be evidence to me and to my future collaborators of development that I have made in my career as a researcher. This project and the Honors contracts that preceded it have been responsible for creating friendships and opportunities that changed my life.

The submission of my capstone project occurred during the Covid-19 global pandemic. This time period disrupted the rhythm of my senior year, making graduation seem somewhat anti-climactic. I feel that submitting my Honors project is the moment that symbolizes my graduation. This project has been the focus of my efforts for only one year of my undergraduate career, but many of the skills required to engage in this project were obtained before its conception. In this

project I used my knowledge of programming in R, operating a linux terminal through ssh, Git version control, and embedding code in org emacs. I learned these skills over the past three years, and I made good memories while I learned them. I met every week with Dr. Pearse and the USU Biology Nerd Herd to gain exposure to research-oriented software and embedded systems. I audited classes that would benefit my research. I came to school early, and I walked home late at night. Submitting this project is the way that I choose to honor those memories and sacrifices as I prepare to graduate to the next stage of life.