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Joshua Castro
University of Central Florida

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MODELING AND ANALYSIS OF A THREE-SPECIES FOOD WEB WITH FACILITATED AND INTRAGUILD PREDATION

by

JOSHUA CASTRO
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ABSTRACT

Biotic interactions are known to shape natural community assemblages and biodiversity. Positive interactions such as facilitation have recently received attention in ecological food webs. Mechanistic models have improved our understanding of these complex food web interactions. Here, focus is given to a three-species food web system with a beach dune natural community in mind. In the last decade, there has been a series of studies investigating intraguild predation between two major loggerhead sea turtle nest predators, North American raccoons and Atlantic ghost crabs. Studies have also highlighted that ghost crab predation assists raccoons in finding nests (i.e., facilitated predation). However, the combined effects of these two intraguild interactions and their consequences on nests have not been examined explicitly. The aims of this study were to (i) develop a three-species, ordinary differential equation model (ii) implement a sensitivity analysis to understand the influence of facilitation and other factors in driving species richness and abundance and (iii) characterize the dynamic interactions between intraguild predators and their effects on a shared resource. Interactions between ghost crabs and sea turtle eggs and facilitation can yield a wide variety of species abundance responses and were influential factors in the model. I found that high secondary sea turtle egg depredation and low facilitated predation by raccoons led to three species co-existence regions in the model. Controlling for nest predators at higher abundance levels showed that ghost crabs had a larger negative effect on sea turtle egg abundance responses when compared to raccoons. This suggests that interactions between sea turtle eggs and ghost crabs appear to be important and potential sea turtle nest management implications are discussed such as the use of ghost crab exclusion devices.

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1. INTRODUCTION

Biotic interactions are known to shape community assemblages and biodiversity (Cornell and Lawton 1992; Morrin 1999). Historically, much focus has been given to competition and predation (Goldberg and Barton 1992; Gurevitch et al. 1992; Sih et al. 1985). More recently, attention has been given to facilitation as a community driver (Callaway 2007; Meyer and Byers 2005; Soliveres et al. 2015), especially in plant communities (Butterfield 2009). Some studies (He et al. 2013; Oviedo et al. 2014) have posited that facilitation is more apparent in stressed habitats allowing for species co-existence.

Food webs are more complex than two species predator-prey systems and studies of interactions among multiple predators and the effects on shared prey have been conducted (Huxel 2007; Losey 1998; Polis et al. 1989; foodwebs.org). Predation on the basal resource by the top predator facilitated by the intermediate predator is defined as facilitated predation (Brown 2009; Cloutier 1997). Fodrie et al. (2008) at Dauphin Island Sea Lab in Alabama, showed that facilitated predation exists in a three species system involving a shared prey, eastern oysters (*Crassostrea virginica*), and two of its main consumers: southern oyster drills (*Stramonita haemastoma*) and stone crabs (*Menippe adina*). Field experiments and laboratory trials demonstrated that when drills and crabs foraged together there was enhanced mortality of oysters. The mechanism for this interaction was due to crabs facilitating drills by breeching oyster valves and granting easy access for drills to their prey.

Here, focus is given to three beach dune species, loggerhead sea turtles (*Caretta caretta*), Atlantic ghost crabs (*Ocypode quadrata*) and North American raccoons (*Procyon lotor*). The loggerhead sea turtle was designated as endangered by the International Union for Conservation of Nature (IUCN 1996). Sea turtles face many anthropogenic (e.g., incidental fisheries by-catch, vessel strikes, oil pollution) and natural (e.g., predation, tidal inundation, disease) threats throughout all of their life stages which contribute to a decline in population numbers. A response to mitigate these losses for the Northwest Atlantic loggerhead population has resulted in a recovery plan with that includes minimizing nest depredation (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008).

Different nesting beaches in the Southeastern United States have different predators of loggerhead nests including: Atlantic ghost crabs (*Ocypode quadrata*), North American raccoons (*Procyon lotor*), coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), armadillos (*Dasypus novemcinctus*) and red imported fire ants (*Solenopsis invicta*) (Allen et al. 2001; Dodd 1988; Engeman et al. 2005). Furthermore, dune vegetation roots (*Uniola paniculata*) are also known to invade nests and in essence depredate on sea turtle eggs (Hannan et al. 2007). On some beaches nest predators can have an extremely negative effect on sea turtle hatching success. For example, in the absence of protective buried wire screens around nests at Canaveral National Seashore, Florida, sea turtle nest loss to predation was as high as 97% (McMurtray 1986).

Raccoons are intraguild predators of ghost crabs in this system (Barton and Roth 2007, 2008). Intraguild predation is when one predator preys on another that it competes with for a common resource (Polis et al. 1989). Ghost crabs are known to burrow into sea turtle nests to feed on eggs; chemical cues emitted through the burrow signal foraging raccoons towards the nest’s location, thereby facilitating secondary depredation of eggs by raccoons (Brown 2009). By directly modulating the availability of resources to other species by causing physical state changes in abiotic materials, in this case tunneling, ghost crabs can be considered to be ecosystem engineers (Jones et al. 1994).

Previous studies have modeled three-species systems using ordinary differential equations and have examined their dynamic behavior. In a three-species food chain model with non-linear functional responses, nutrient enrichment had adverse effects on higher level consumers (Abrams and Roth 1994). Gilpin (1979) looked at a one predator-two prey community interaction model developed by Vance (1978) and was able to find chaotic behavior. Three species intraguild predation models have been developed (Holt and Polis 1997) and model extensions such as alternative prey have been explored (Holt and Huxel 2007). Here I simulate the effects of facilitated predation in a three-species intraguild predation model.

The aims of this study were to (i) develop a three-species, ordinary differential equation model (ii) implement a sensitivity analysis to understand the influence of facilitation and other factors in driving species richness and abundance and (iii) characterize the dynamic interactions between intraguild predators, where one species facilitates resource acquisition, and the overall effects on a shared resource.

2. METHODS

2.1 Model Development

An ordinary differential equation model was constructed in order to characterize the dynamic interactions between species with both intraguild predation and intraguild facilitation and their effects on a shared resource. Software packages STELLA version 9.0 and R were used to develop the model. The initial model formulation was derived from a generic food-web point of view that involves resource, prey, and consumer species. It was altered to replicate the intraguild predation and intraguild facilitation interactions as depicted by the sea turtle egg, ghost crab and raccoon system (Figure 1). The model was a slight expansion of Lotka-Volterra equations depicting three interacting species.

$$\frac{dx_1}{dt} = (r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3 - da_{12}x_2x_3)x_1 \qquad (1)$$

$$\frac{dx_2}{dt} = (r_2 - a_{22}x_2 + a_{21}x_1 - a_{23}x_3)x_2 \qquad (2)$$

$$\frac{dx_3}{dt} = (r_3 - a_{33}x_3 + a_{31}x_1 + a_{32}x_2 + fa_{12}x_2x_1)x_3 \qquad (3)$$

The above equations describe the rates of population change, where x_1 represents resource abundance (eggs), x_2 represents prey abundance (ghost crabs) and x_3 represents consumer (raccoon) abundance. The symbols r_1, r_2 and r_3 represent growth rates for the resource, prey and consumer respectively. The symbols $a_{11} – a_{33}$ represent interaction coefficients among the three species. For example, a_{12} represents the effect of species 2 on the per capita growth rate of species 1. Interaction coefficients can be written as a community matrix *C*, where the absolute value of the coefficient indicates the relative species effect and the sign indicates direction (Levins 1968).

$$C = \begin{bmatrix} -a_{11} & -a_{12} & -a_{13} \\ +a_{21} & -a_{22} & -a_{23} \\ +a_{31} & +a_{32} & -a_{33} \end{bmatrix} \tag{4}$$

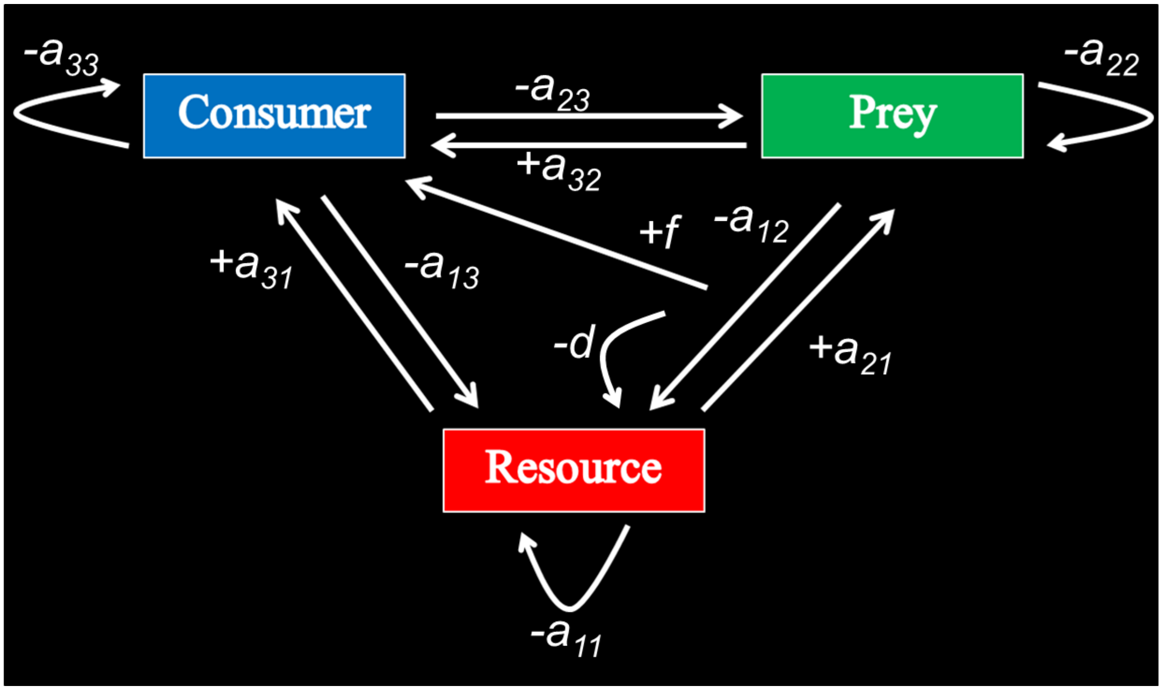


Figure 1. Interaction di-graph showing model structure. Direction of arrows indicate the species being affected and sign indicates a positive or negative interaction. Parameters *d* and *f* represent depredation and facilitation proportionalities.

The term $a_{12}x_1x_2x_3$ in the resource and consumer equations represent indirect effects of prey and is a function of resource, prey, and consumer abundance. All three species are involved because they interact with each other and $x_1x_2x_3$ indicates random encounters of resources, prey and consumers. Interaction coefficient a_{12} is included in this term because the indirect effect involves resource and prey.

The term $a_{12}x_1x_2x_3$ is additive in the model and can affect the resource and consumer differently and is distinguished by symbols d and f. The probability of secondary depredation of the resource by the consumer is represented as d. This is intended to represent additional losses to the resource. Symbol f represents the degree of facilitation of the consumer due to the presence of the prey feeding on the resource. This is intended to represent additional gains to consumer abundance.

To reflect the sea turtle egg, ghost crab and raccoon system, I derived model parameters from previously published field studies, whenever possible. Otherwise, I made educated guesses based on estimated relative population sizes and assumed autecological properties. Parameter values and their potential ranges are listed in Table 1. Values of interaction coefficients ($a_{11} - a_{33}$) are relative to each other. For example, the effect of sea turtle eggs on ghost crabs is 10 times larger than the effect of sea turtle eggs on raccoons. This is reasonable considering that ghost crabs have a much smaller body size when compared to raccoons. The rest of the interaction coefficients have been estimated using a similar logical approach. Growth rate parameter values were also estimated using this comparative approach. For example, ghost crabs have relatively shorter lifespans than raccoons, and would have a larger growth rate value when compared to raccoons.

Table 1. Parameter abbreviation, estimate, range, unit and reference.

Name	Parameter	Estimate*	Min	Max	Units
x_1	Resource Abundance	10,000 (initial population size)			individuals
x_2	Prey Abundance	100 (initial population size)			individuals
x_3	Consumer Abundance	10 (initial population size)			individuals
a_{11}	Effect of Resource on itself	0.0000001	0.00000001	0.000001	$(x_1^2)^{-1}$
a_{12}	Effect of Prey on Resource	0.000001	0.0000001	0.00001	$(x_1x_2)^{-1}$
a_{13}	Effect of Consumer on Resource	0.000001	0.0000001	0.00001	$(x_1x_3)^{-1}$
a_{21}	Effect of Resource on Prey	0.000001	0.0000001	0.00001	$(x_2x_1)^{-1}$
a_{22}	Effect of Prey on itself	0.00001	0.000001	0.0001	$(x_2^2)^{-1}$
a_{23}	Effect of Consumer on Prey	0.00001	0.0000001	0.0001	$(x_2x_3)^{-1}$
a_{31}	Effect of Resource on Consumer	0.0000001	0.00000001	0.000001	$(x_3x_1)^{-1}$
a_{32}	Effect of Prey on Consumer	0.0000001	0.00000001	0.000001	$(x_3x_2)^{-1}$
a_{33}	Effect of Consumer on itself	0.001	0.0001	0.01	$(x_1^2)^{-1}$
r_1	Resource growth rate	0.05			$x_1[\text{time}]^{-1}$
r_2	Prey growth rate	0.0001			$x_2[\text{time}]^{-1}$
r_3	Consumer growth rate	0.00001			$x_3[\text{time}]^{-1}$
d	Resource secondary depredation proportionality	0.05 (Welicky et al. 2012)	0.01	0.1	unitless
f	Facilitation proportionality for Consumer	0.05 (Brown 2009)	0.01	0.1	unitless
dummy	Dummy variable used for determining significance in eFAST	N/A	1	10	unitless

*Estimates for the resource secondary depredation proportionality parameter *d* were derived from fraction of loggerhead nests depredated per season in Canaveral National Seashore, Florida, 1989-2008. Estimates for the facilitation proportionality parameter *f* were derived from raccoons visiting simulated ghost crab predated loggerhead nests (Brown 2009).

Sea turtle egg growth rate unit is number of eggs laid on beach per unit time and has a larger value than ghost crab and raccoon growth rates. Sea turtle egg abundance was calibrated by using an iterative approach of incrementally adjusting parameters so that the simulated abundance remained within the bounds of realistic abundances per 1 km section of beach.

Simulated sea turtle egg densities varied from 100-200,000 eggs / km of beach depending on parameter values. In Florida, there were on average 88 nests (i.e., combined loggerhead, green turtle, and leatherback) per 1 km survey beach based on statewide nesting beach survey data for the 2013 nesting season (Florida Fish and Wildlife Conservation Commission 2014). On average, loggerheads, green turtles, and leatherbacks lay 112.4, 136, and 73 eggs per clutch respectively (Witherington and Ehrhart 1989a; Miller et al. 2003; Stewart and Johnson 2006). To estimate number of eggs per 1 km section of beach I took the average of the above three clutch sizes, 107 eggs, and multiplied this by number of observed nests to obtain 9,416 eggs. This estimate falls within the bounds of simulated egg abundances. Simulated raccoon abundances varied from 7-15,924 individuals. According to Barton (2005), 56 raccoons were removed from two east-central Florida beaches measuring approximately 36.5 total km in length in 2003. I obtained an estimate of 1 individual per 1 km section of beach by dividing observed raccoon numbers by total beach length. Simulated ghost crab abundances varied from 100-1,600 individuals depending on parameter values. Morrow et al. (2014) observed average densities of 4-14 burrows per 10x10 meter grid among three Florida west coast beaches. I multiplied observed densities by 100 to obtain an estimate of 400-1,400 individuals per 1 km section of beach, which is comparable to simulated abundances.

2.2 Sensitivity Analysis

Sensitivity analysis (SA) seeks to learn how the output of a model changes with variations in the input (Saltelli et al. 2000) and recent techniques have been applied to ecological food web models (Ciric et al. 2012; Saloranta et al. 2006). Following Cariboni et al. (2007) I used a variance-based SA approach because the model has a low number of factors (<20). Due to the non-linearity of the model I chose an extended Fourier Amplitude Sensitivity Test (eFAST) in order to decompose the output variance into the total contributions attributable to each input factor (Cariboni et al. 2007).

The eFAST method is a variance decomposition procedure suited to perform a global, quantitative, model-independent sensitivity analysis (Saltelli et al. 1999). It was adapted from the FAST method (Cukier et al. 1973) in order to include first and total order sensitivity indices. Partitioning the variation of each input parameter works by varying different parameters at different frequencies and encoding each parameter with a unique identity frequency. Fourier analysis then measures the strength of each parameter's frequency in the model output through the use of two indices, S_i and S_{Ti}. S_i is the first-order sensitivity index and represents the fraction of model output variance explained by the input variation of a given parameter i. This index represents main effects and is the variation in the model output explained by the particular parameter alone. S_{Ti} is the total-order sensitivity index and represents the higher-order, non-linear interactions between the parameter of interest and the complementary set of parameters (i.e. all parameters except i) (Marino et al. 2008). The index represents total effects and is the variance explained by the interactions of the particular parameter with all other parameters. A parameter is considered influential if it has a higher index value when compared to other parameters.

Sensitivity analyses were conducted using the R package *spartan* (Alden et al. 2014). The R package *gplots* was also used for assistance in producing figures (Wand 2009). In order to attribute the variance in model outputs to its input factors, sampling of the possible parameter space was first conducted. This was done by assigning values to each parameter chosen from a Fourier frequency search curve through a parameter's potential range of values given in Table 1. Although all parameters are perturbed simultaneously, focus is given to one parameter by assigning it a sampling frequency different from the other parameters. A set of simulation input parameters then exists for each parameter. The given parameter's sampling frequency is then adjusted and resampling is conducted on a new search curve. There were a total of three search curves for my analysis. There are no guidelines to follow regarding sample size N_S, but the minimum must be greater than 65 (Saltelli et al. 1999).

The total number of simulation runs N equals the product of the number of parameters k, number of samples and number of search curves N_R, $N = N_S \times k \times N_R$ (Saltelli et al. 1999). In my analysis I had 3 search curves with each curve initially taking 65 samples for each of the 12 parameters of interest for a total of 2,340 parameter sets used as inputs for simulation runs. Uniform distributions were assumed for all model parameters within the minimum to maximum ranges (Saltelli et al. 2000). A uniform distribution was used as a conservative choice due to the absence of prior information about parameter distributions (Ciric et al. 2012).

Input parameter sets from sampling were then run through the model and the output measures x_1, x_2, and x_3 were stored. I utilized the R package *deSolve* (Soetaert et al. 2010) which includes a numerical ordinary differential equation solver using the 4th order Runge-Kutta method. Output measures were stored as a time-series with a total of 2,000 time steps.

Medians from each of the initial 2,340 simulation run outputs were then calculated using the *spartan* algorithm. A summary file was then created for each resampling curve, summarizing the medians of the initial 65 parameter sample output measures attributed to a parameter. These distribution data were then used to partition the output variance to input parameters.

Sensitivity indices are obtained using the unique frequency assigned to a particular parameter and calculating the contribution to the model variance due to that parameter. First-order indices using the classical FAST approach calculates the unique model variance due to a parameter. The total-order sensitivity indices are obtained by considering the residual variance that is not accounted for by the first-order indices (Saltelli et al. 2000). *P*-values were assigned to indices using a two-sample *t*-test by comparing the distribution of a parameter of interest to that of the dummy parameter's distribution. The dummy parameter has zero effect on the model output and was used to establish significance among parameters.

Sensitivity tests were conducted with sample sizes larger than 65 (i.e., N_S =1025 and 2049) and differences were observed in sea turtle egg abundance total sensitivity indices (Figure 2). Most indices seemed to converge and their standard errors decreased as sample size increased. Thus the largest sample size of 2,049 was used to test the parameter sensitivities, which led to 73,764 model evaluations. Sensitivity tests were also evaluated at different time spans in the model (t=50, 100, 150, 200) and no large differences were observed in sensitivity indices. A time span of 200 was used to evaluate the parameter sensitivities.

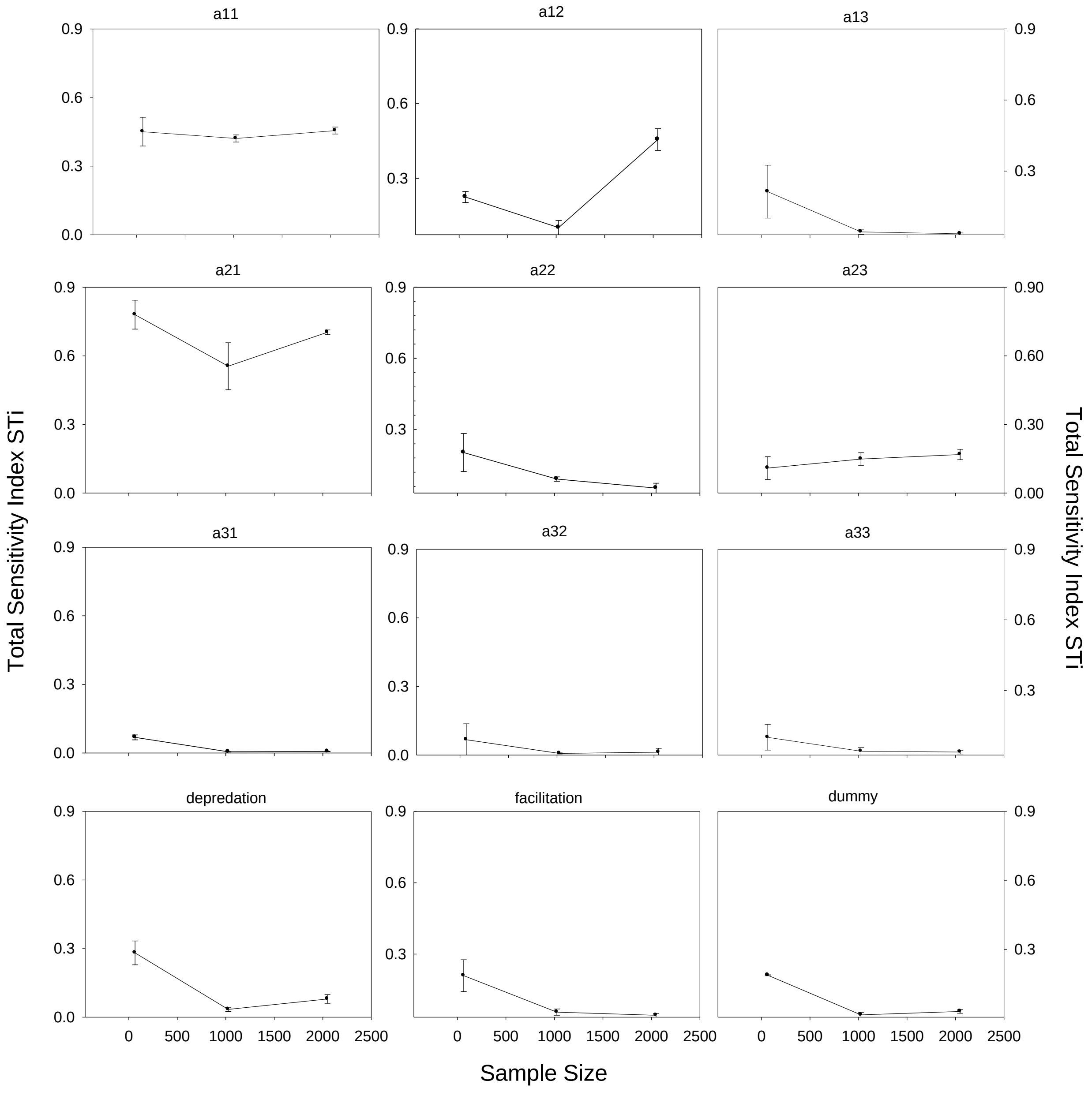


Figure 2. Relationship of the total sensitivity index for sea turtle egg abundance against the number of samples taken (N_s = 65, 1025, 2049) within the range of the twelve parameters in the model with 200 time steps.

2.3 System Dynamics

In order to understand the behavior of this system more fully, I also explored the parameter space defined by the facilitation and depredation by manipulating these variables individually. Model behaviors were characterized by incrementally adjusting parameters *d* and *f* one-at-a-time. One parameter was kept constant, while the other was being sampled. Uniform sampling was conducted across the parameter's range resulting in 100 samples.

I categorized the possible model behaviors as being either stable focus, stable limit cycles, aperiodic, or extinction. Stable focus means that output trajectories converge onto an equilibrium point (Upadhyay and Raw 2011). Stable limit cycle behavior means that output trajectories converge onto a stable orbit or oscillation between the maximum and minimum output values. Aperiodic behavior is characterized by no apparent pattern in the oscillations between the maximum and minimum output values. Extinction is when one or more output trajectories reach zero.

2.4 Control Scenarios

Recognizing that the derived parameters (Table 1) are probably unrealistic, I still wanted to evaluate the behavior of the system as a consequence of potential management scenarios. As resource managers are concerned with protecting the endangered sea turtles, I investigated how controlling for the different nest predators (ghost crab and raccoon) affects sea turtle egg abundance. To understand this, nest predator abundances were held constant at low, medium and high levels. In the first scenario, ghost crab abundance was held constant at 10, 100 and 250 individuals. Parameter values used in these simulations are given in table 1. In the second scenario, raccoon abundance was held constant at 10, 1,000 and 10,000 individuals and parameter values used are in Table 1. In order to produce a noticeable response, high raccoon abundances were used.

3. RESULTS

3.1 Sensitivity Analysis

Sensitivity indices and their associated errors were produced for all parameters of interest (Table 2; Figures 3, 4 & 5). Rankings were assigned to factors influencing species abundances (Table 3).

Total-order sensitivity index for interaction coefficient a_{11} was significant in producing variance in sea turtle egg abundance (S_{Ti}=0.455, P<0.001). Parameter a_{11} represents the interaction effects of sea turtle eggs on themselves. This limits increases in sea turtle egg abundance. Interaction coefficient a_{21} was significant in producing variance in sea turtle egg abundance (S_i=0.307, P=0.001; S_{Ti}=0.703, P<0.001). The interaction coefficient a_{21} represents the effect of sea turtle eggs on ghost crabs and it enhances population ghost crab growth due to sea turtle egg consumption. Such high S_i and S_{Ti} values indicate that ghost crab abundance is influential in reducing sea turtle egg abundance in the model. The interaction coefficient a_{21} was the most influential factor in the model. Small changes in a_{21} cause considerable variance to sea turtle egg abundance, indicating that sea turtle egg abundance is very sensitive to a_{21}. The interaction coefficient a_{23} was significant in producing variance in sea turtle egg abundance (S_i=0.061, P=0.019; S_{Ti}=0.168, P=0.008). The depredation parameter d was significant in producing variance in sea turtle egg abundance (S_i=0.019, P=0.038; S_{Ti}=0.079, P=0.038).

Table 2. Partitioning of variance values in simulated resource, prey and consumer abundances to input interaction coefficients, nest depredation and facilitation parameters for both their main S_i and total effect S_{Ti}. Significant parameters and associated values (P<0.05) are in bold.

Parameter	S_i±SE	P	S_{Ti}±SE	P
Resource x_1				
a_{11}	**0.107±0.006**	0.002	**0.455±0.015**	<0.001
a_{12}	0.046±0.026	0.067	0.093±0.044	0.079
a_{13}	**0.004±0.001**	0.008	0.035±0.003	0.335
a_{21}	**0.307±0.014**	0.001	**0.703±0.010**	<0.001
a_{22}	**0.015±0.004**	0.027	0.053±0.021	0.132
a_{23}	**0.061±0.013**	0.019	**0.168±0.023**	0.008
a_{31}	0	0.468	0.006±0.001	0.951
a_{32}	0	0.165	0.012±0.017	0.634
a_{33}	**0.002**	0.003	0.038±0.008	0.165
d	**0.019±0.006**	0.038	**0.079±0.019**	0.038
f	**0.001**	0.024	0.043±0.008	0.087
dummy	0	N/A	0.030±0.008	N/A
Prey x_2				
a_{11}	**0.008±0.003**	0.041	0.086±0.027	0.089
a_{12}	**0.231±0.009**	0.001	**0.640±0.012**	<0.001
a_{13}	**0.001±0**	0.012	0.032±0.004	0.707
a_{21}	**0.125±0.011**	0.003	**0.277±0.012**	<0.001
a_{22}	**0.053±0.006**	0.005	**0.323±0.046**	0.012
a_{23}	0.003±0.005	0.1	0.130±0.024	0.083
a_{31}	0	0.978	0.061±0.022	0.524
a_{32}	0	0.716	0.018±0.003	0.884
a_{33}	**0.040±0.008**	0.016	**0.119±0.012**	0.01
d	**0.011±0.002**	0.013	0.085±0.003	0.048
f	0.075±0.056	0.054	**0.231±0.066**	0.023
dummy	0	N/A	0.032±0.015	N/A
Consumer x_3				
a_{11}	**0.091±0.006**	0.002	**0.284±0.022**	0.006
a_{12}	**0.002±0.001**	0.042	0.080±0.017	0.957
a_{13}	**0.023±0.002**	0.003	0.167±0.031	0.350
a_{21}	**0.016±0.001**	0.004	**0.217±0.020**	0.039
a_{22}	0.002±0.001	0.045	0.045±0.012	0.983
a_{23}	0.004±0.002	0.085	0.144±0.032	0.535
a_{31}	0	0.147	0.061±0.008	0.974
a_{32}	0	0.299	0.114±0.032	0.859
a_{33}	**0.208±0.039**	0.014	**0.437±0.012**	<0.001
d	**0.159±0.016**	0.005	**0.408±0.012**	0.001
f	**0.138±0.017**	0.007	**0.276±0.019**	0.007
dummy	0	N/A	0.157±0.024	N/A

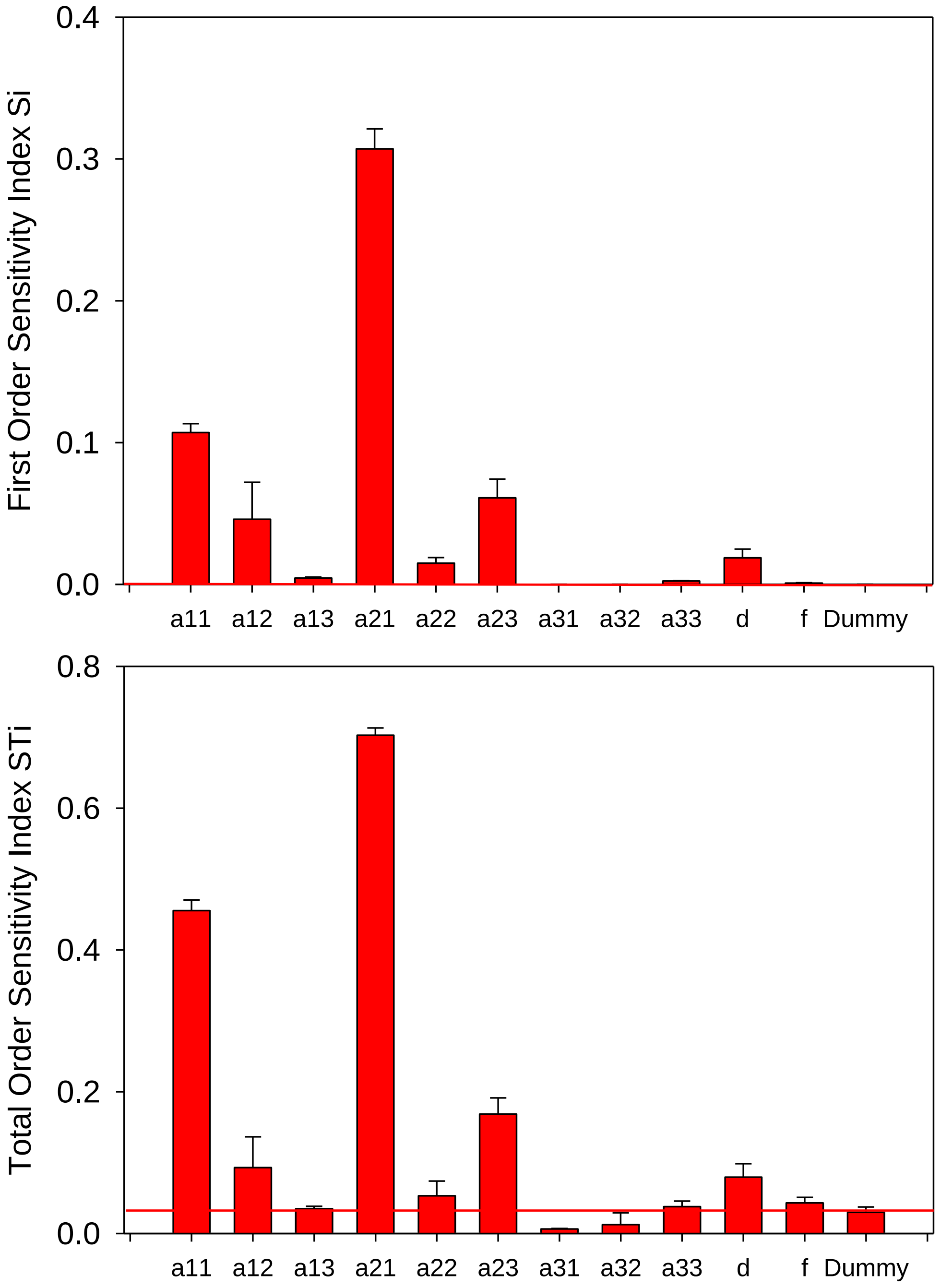


Figure 3. Proportion of total sea turtle egg abundance x_1 variance explained by 12 model parameters analyzed using the eFAST method. The top panel represents main effects and is the variance explained by the particular parameter alone. The bottom panel represents total effects and is the variance explained by the interactions of the particular parameter with all other parameters. Parameter values larger than the dummy (red line) were considered significant.

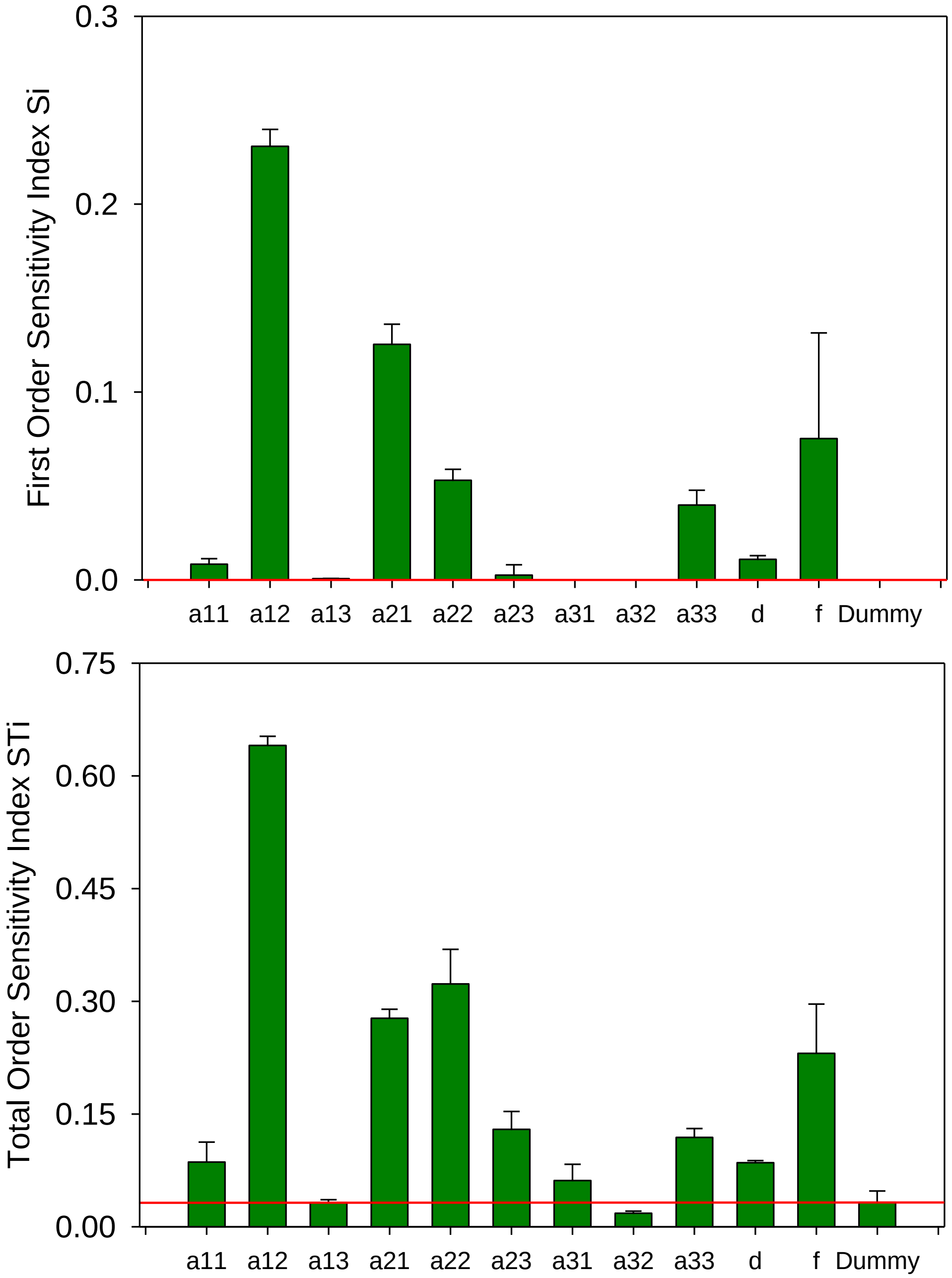


Figure 4. Proportion of total ghost crab abundance variance x_2 explained by 12 model parameters analyzed using the eFAST method. The top panel represents main effects and is the variance explained by the particular parameter alone. The bottom panel represents total effects and is the variance explained by the interactions of the particular parameter with all other parameters. Parameter values larger than the dummy (red line) were considered significant.

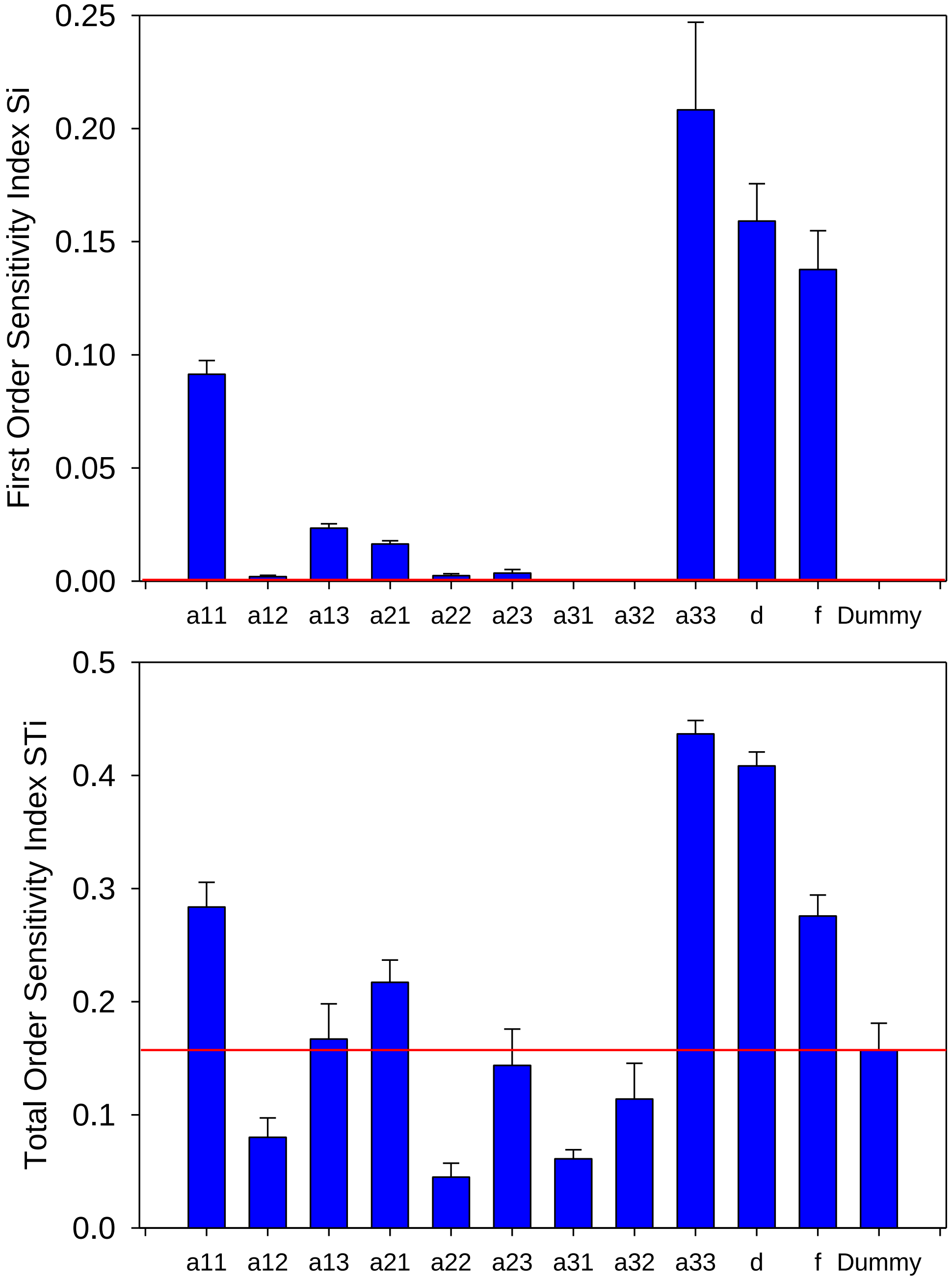


Figure 5. Proportion of total raccoon abundance x_3 variance explained by 12 model parameters analyzed using the eFAST method. The top panel represents main effects and is the variance explained by the particular parameter alone. The bottom panel represents total effects and is the variance explained by the interactions of the particular parameter with all other parameters. Parameter values larger than the dummy (red line) were considered significant.

Table 3. Factor ranking of species abundances based on eFAST total effect index. Boldened variables are considered to be significant. Those in yellow were consistently significant among the three species.

Rank	Sea Turtle Egg Abundance	Ghost Crab Abundance	Raccoon Abundance
1	**a_{21}**	**a_{12}**	**a_{33}**
2	**a_{11}**	**a_{22}**	**d**
3	**a_{23}**	**a_{21}**	**a_{11}**
4	**a_{12}**	**f**	**f**
5	**d**	**a_{23}**	**a_{21}**
6	**a_{22}**	**a_{33}**	**a_{13}**
7	**f**	**a_{11}**	*dummy*
8	**a_{33}**	**d**	a_{23}
9	**a_{13}**	**a_{31}**	a_{32}
10	*dummy*	**a_{13}**	a_{12}
11	a_{32}	*dummy*	a_{31}
12	a_{31}	a_{32}	a_{22}

Raccoon predation on sea turtle eggs a_{31} was not significant in producing variance in sea turtle egg abundance (S_i=0, P=0.468; S_{Ti}=0.006, P=0.951).

Ghost crab predation on sea turtle eggs a_{12} had a significant effect on ghost crab abundance (S_i=0.231, P=0.001; S_{Ti}=0.640, P=<0.001). The interaction coefficient a_{12} was the most influential parameter for ghost crab abundance. The energy ghost crabs gain from sea turtle egg predation a_{21} had a significant effect on ghost crab abundance (S_i=0.125, P=0.003; S_{Ti}=0.277, P=<0.001). The effect of ghost crabs on itself a_{22} also had a significant effect on ghost crab abundance (S_i=0.053, P=0.005; S_{Ti}=0.323, P=0.012). The facilitation parameter had a significant effect on ghost crab abundance (S_i=0.231, P=0.023).

The effect of sea turtle eggs on itself a_{11} had a significant effect on raccoon abundance (S_i=0.091, P=0.002; S_{Ti}=0.284, P=0.006). The effect of raccoons on itself a_{33} had a significant effect on raccoon abundance (S_i=0.208, P=0.014; S_{Ti}=0.437, P=<0.001). This was the most influential parameter for raccoon abundance. Secondary depredation d of sea turtle nests by raccoons had a significant effect on raccoon abundance (S_i=0.159, P=0.005; S_{Ti}=0.408, P=0.001). The facilitation parameter f had a significant effect on raccoon abundance (S_i=0.138, P=0.007; S_{Ti}=0.276, P=0.007).

Interaction coefficients a_{11}, a_{13}, a_{21}, a_{33}, facilitation parameter f, and the depredation parameter d were consistently important for all three species (Table 3).

3.2 System Dynamics

Rich dynamics in this system were initially discovered by varying facilitation and depredation parameter values one-at-a-time, while keeping other parameter values constant. The values of the facilitation parameter *f* was varied across the range [0.01-0.99] and consistently led to stable focus. Varying depredation parameter *d* led to stable focus, stable limit cycles and extinction (Table 4).

The model generated a wide range of behaviors. Regions of stable focus were found for sea turtle eggs, ghost crabs and raccoons (Figure 6). Regions of stable limit cycles were found for raccoons and ghost crabs. This led to oscillations in abundances (Figure 7). Aperiodic regions were found with three species co-existence. There was no pattern of the limits of maximum and minimum abundances within these regions (Figure 8). Regions of extinction were found for raccoons. Regions of extinction for ghost crabs were not found. Low secondary sea turtle egg depredation and high facilitation values led to extinction regions in the model (Figure 9).

The parameter space was explored by further varying depredation and facilitation parameter values simultaneously. Depredation and facilitation parameter values were varied in the range [0-1] at 0.1 intervals (Figure 10a). Stable focus regions were found with three species co-existence. Extinction regions were also found with two species co-existence. In order to find more dynamic regions depredation parameter values were varied in the range [0.001-0.02] at 0.0025 intervals and facilitation parameter values were varied in the range [0-1] at 0.1 intervals (Figure 10b). Depredation values greater than 0.015 and facilitation values less than 0.3 led to stable focus regions (Figure 10b). In general, high secondary sea turtle egg depredation and low facilitation values led to stable focus behaviors from the model.

Table 4. Dynamical outcomes for model system (Equations 1-3). Parameter values were kept constant (see Table 1) except for the facilitation (*f*) and depredation (*d)* multipliers. Representative dynamical outcome simulations are provided (Figures 6, 7, 8, & 9).

Parameter varied	Range in which parameter was varied	Dynamical Outcome
f	0.01-0.99	Stable focus
d	0.001-0.002	Extinction
	0.003-0.01	Stable limit cycle
	0.02-0.99	Stable focus

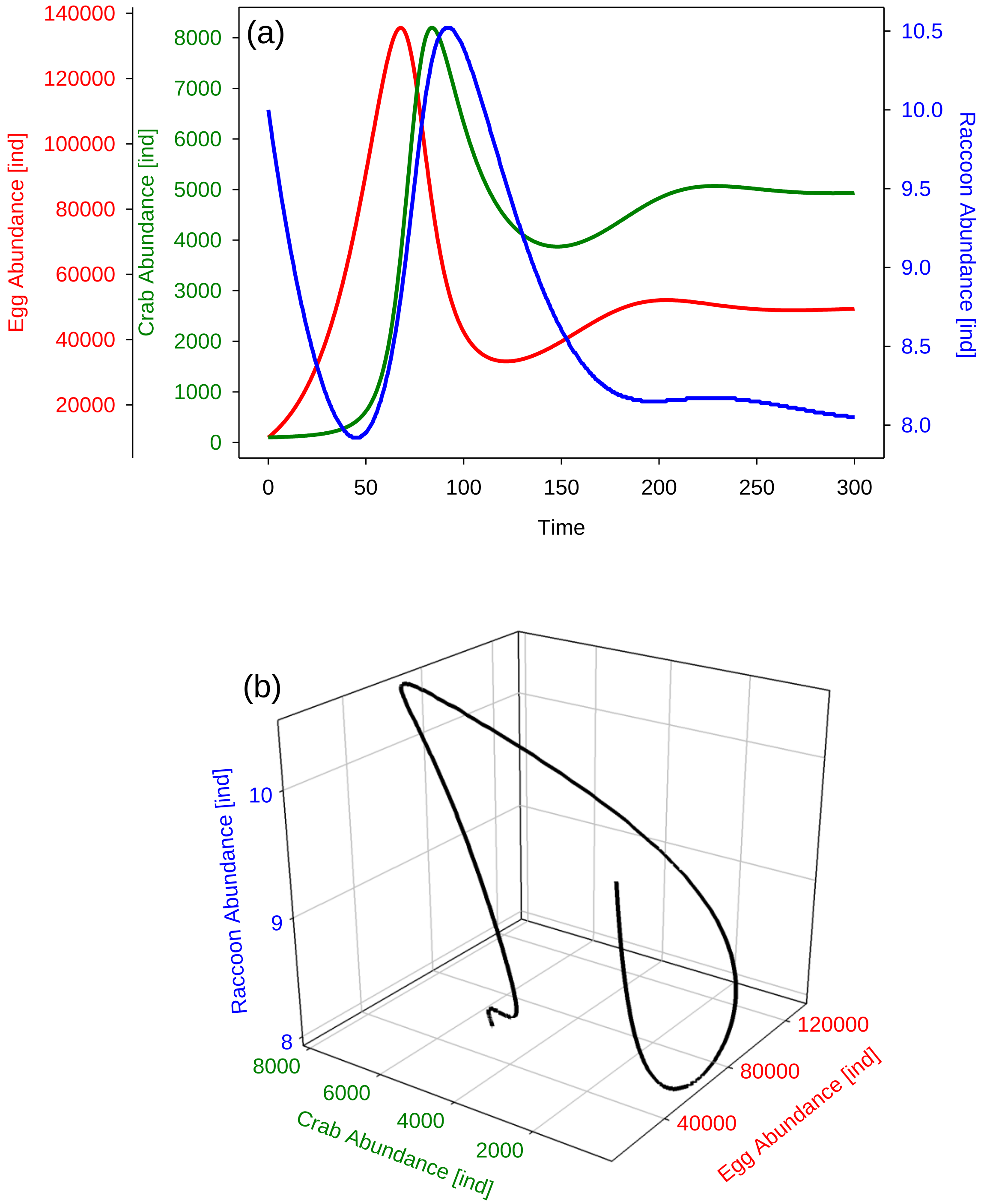


Figure 6. (a) Trajectories for an example of a stable focus for species abundances; (b) Corresponding phase plane plot of a stable focus. (*d*=1, *f*=0.0001)

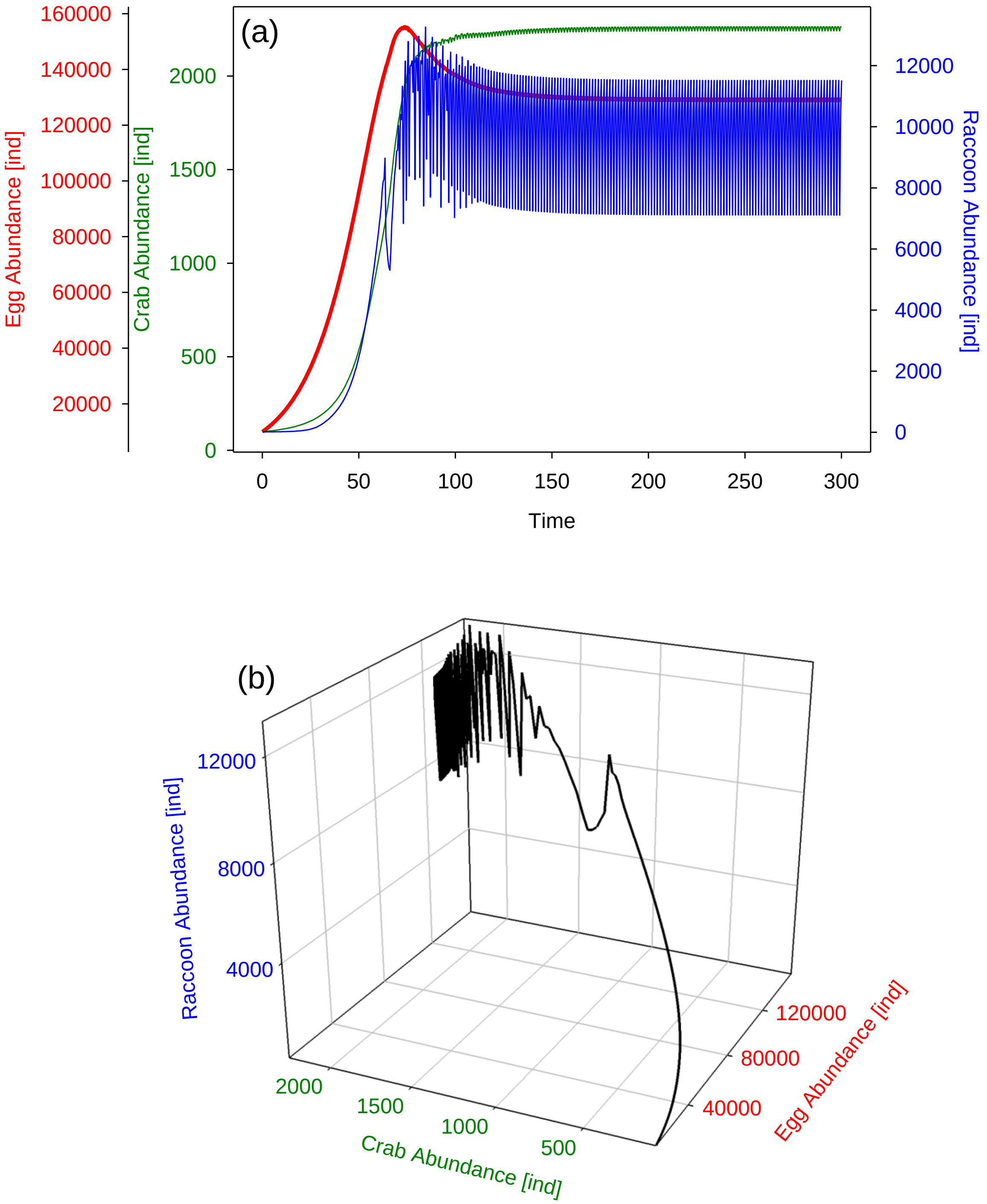


Figure 7. (a) Trajectories for an example of a stable limit cycle for abundances of model system; (b) Corresponding phase plane plot of a stable limit cycle. (*d*=0.5, *f*=0.05)

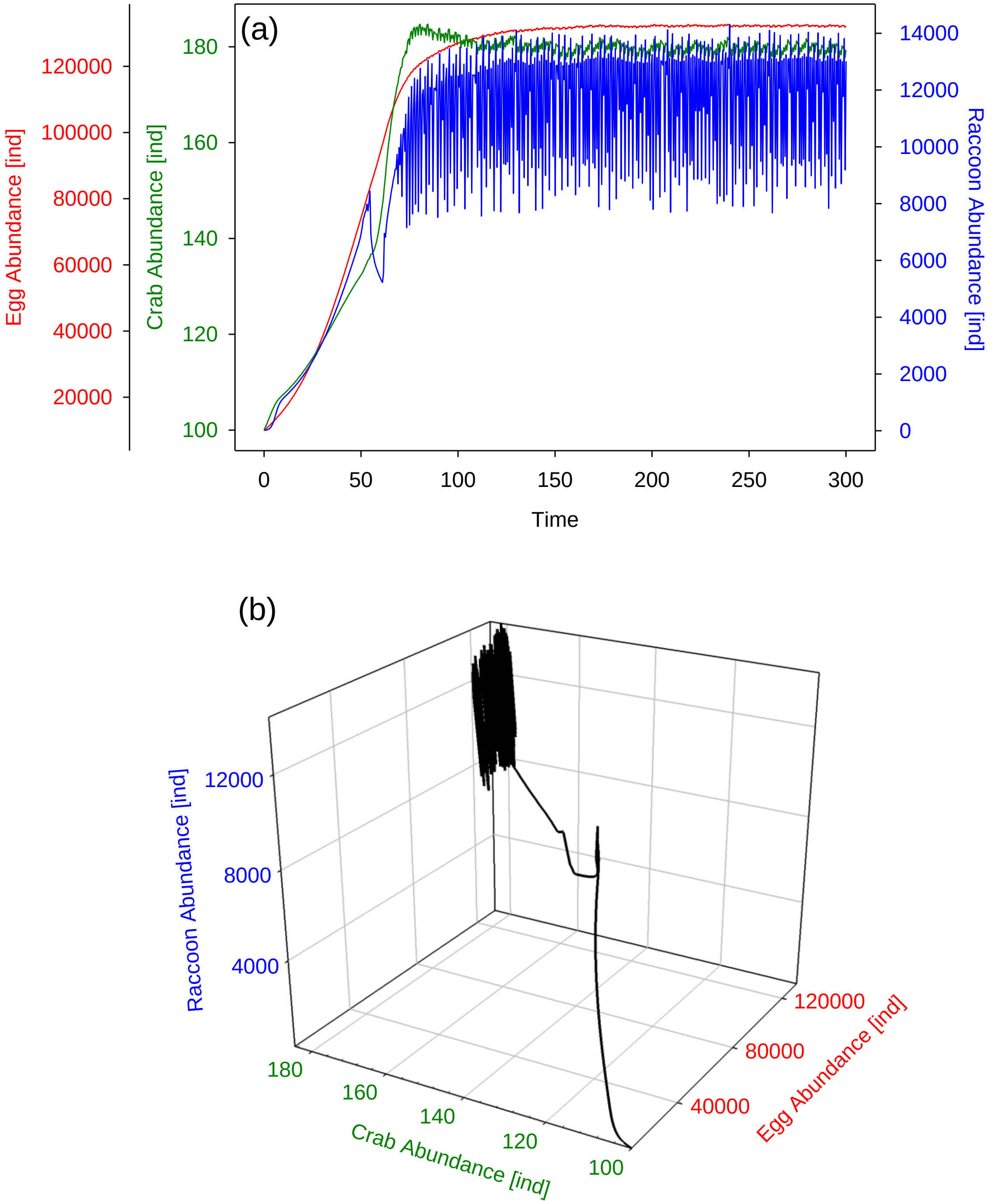
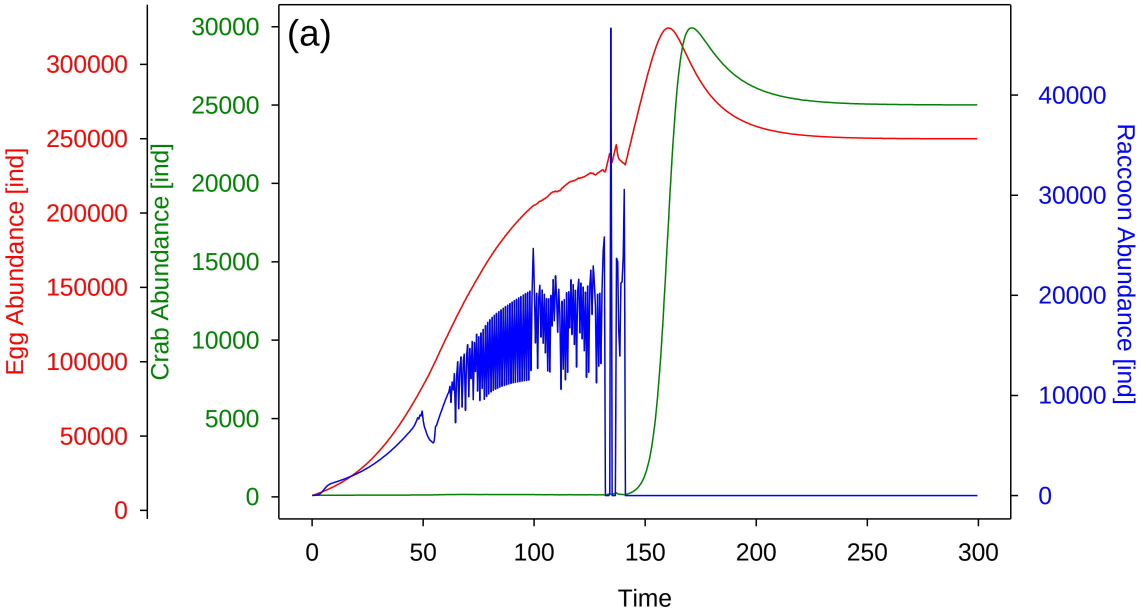


Figure 8. (a) Trajectories for an example of aperiodic behavior for abundances of model system; (b) Corresponding phase plane plot of aperiodic behavior. (d=0.01, f=0.7)



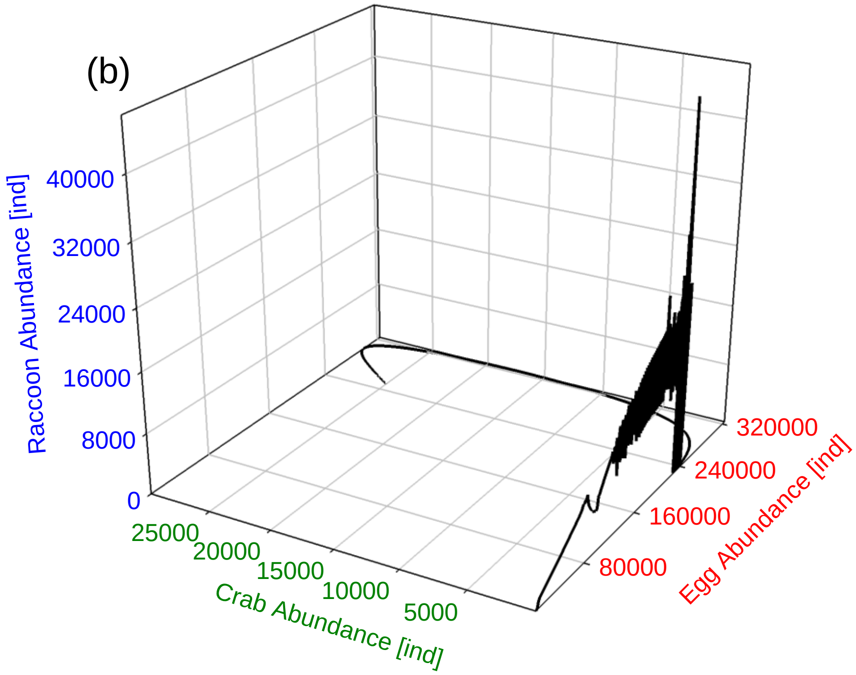


Figure 9. (a) Trajectories for an example of extinction for abundances of model system; (b) Corresponding phase plane plot of extinction. Raccoon populations go extinct. (*d*=0.001, *f*=0.8)

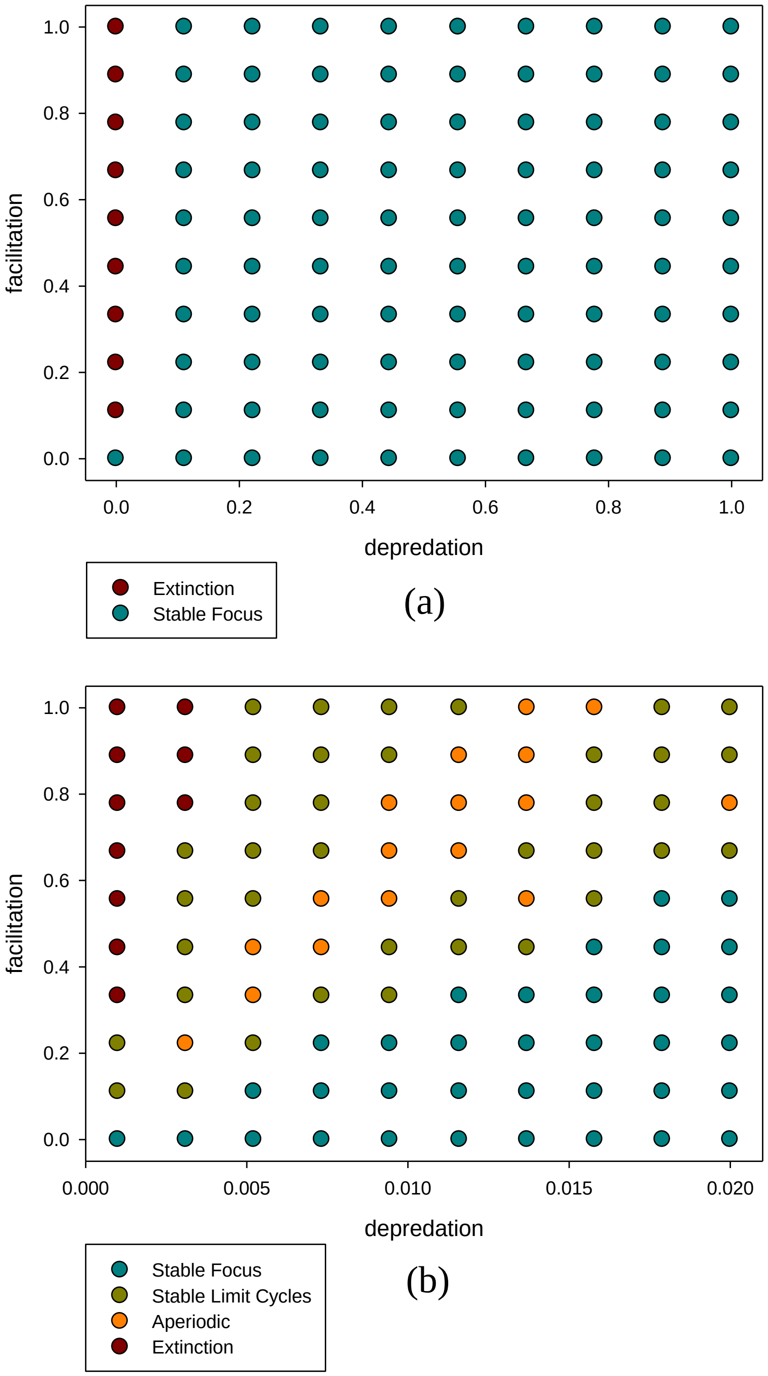


Figure 10. Parameter space of depredation and facilitation parameters. In (a) depredation and facilitation values are both varied in the range [0-1]. In (b) depredation values vary between [0.001-0.02] and facilitation values vary between [0-1].

3.3 Ghost Crab Control Scenario

Controlling for ghost crabs caused sea turtle egg abundance to increase for all three levels in the model. Controlling for ghost crabs at low abundances (x_2=10) caused sea turtle egg and raccoon abundances to asymptotically approach a plateau (Figure 11a). The plateau value for sea turtle eggs for the smallest crab population was larger than found with the medium (x_2=100) and high (x_2=250) crab population levels. Controlling for ghost crabs at medium abundance levels caused sea turtle egg and raccoon abundances to approach a plateau asymptotically rather than overshooting it then stabilizing had ghost crab abundance not been constant (Figure 11b).

At the high ghost crab abundance level, sea turtle egg and raccoon abundances increased rapidly at first, then decreased and approached a plateau value smaller than the low and medium ghost crab control abundances (Figure 11c). Comparison between the two nest predators showed that high ghost crab numbers had a larger effect on sea turtle eggs than high raccoon numbers.

3.4 Raccoon Control Scenario

Similar to the ghost crab control scenario, controlling for raccoons led to increased sea turtle egg and ghost crab abundances for all three levels in the model. Controlling for raccoons at the low abundance (x_3=10) caused sea turtle egg and ghost crab abundances to increase logistically and approach a higher level than medium and low ghost crab control levels (Figure 12a). At a medium control level (x_3=1,000), sea turtle egg and raccoon abundances increased then decreased slightly and approached a plateau (Figure 12b). At the high raccoon control level (x_3=10,000), sea turtle egg and ghost crab abundances oscillated around a value smaller than low and medium levels (Figure 12c).

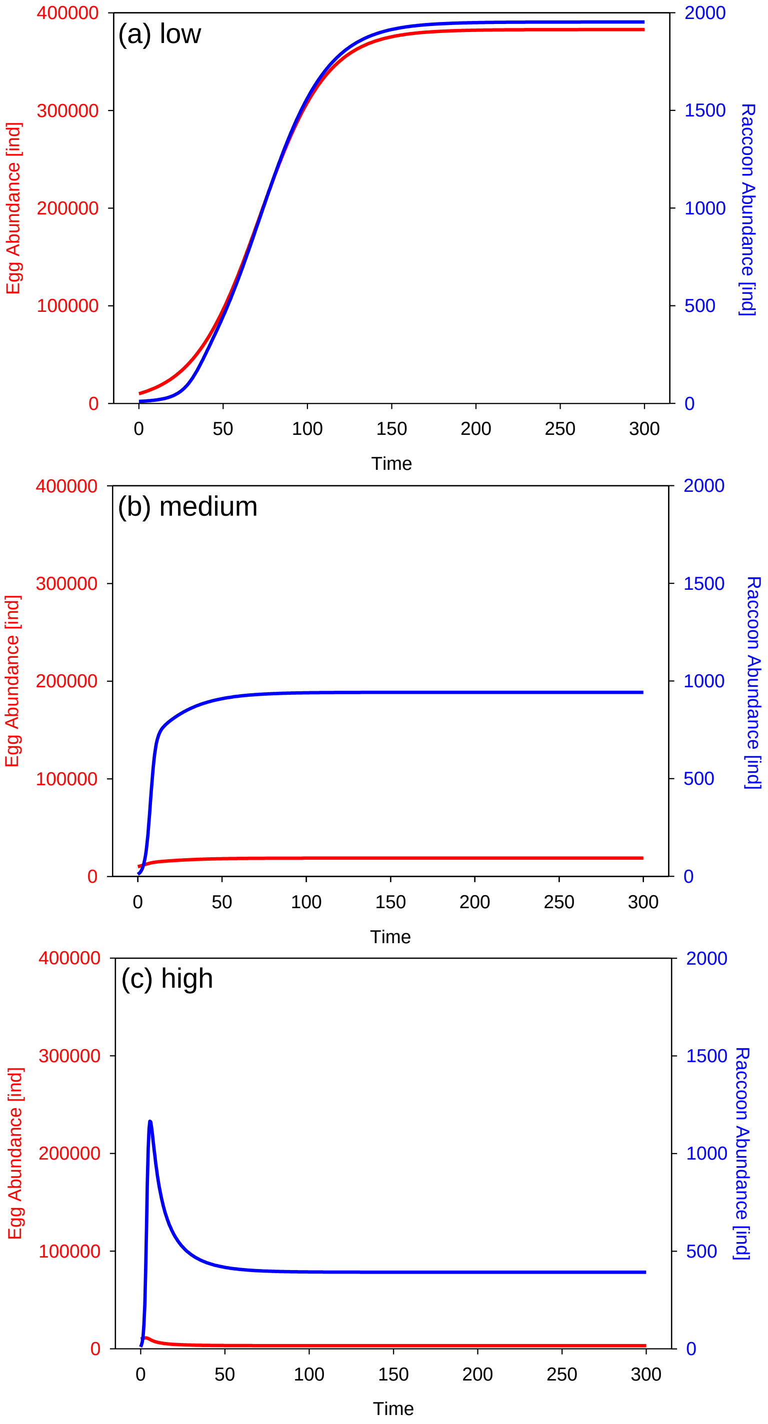


Figure 11. The effects of sea turtle nest predator control on simulated abundances. Ghost crab abundances were held constant at (a) low (10 individuals), (b) medium (100 individuals) and (c) high (250 individuals) levels.

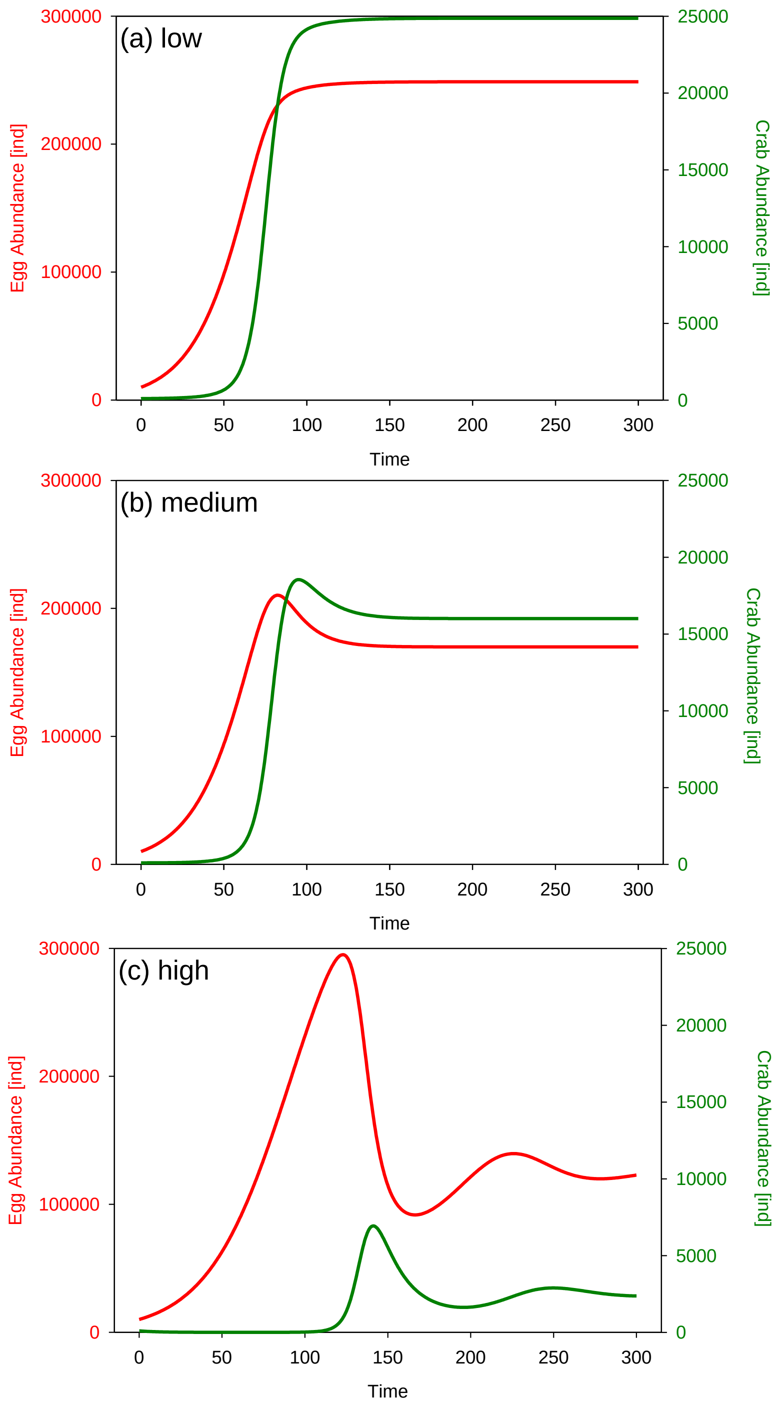


Figure 12. The effects of sea turtle nest predator control on simulated abundances. Raccoon abundances were held constant at (d) low (10 individuals), (e) medium (1,000 individuals) and (f) high (10,000 individuals) levels.

4. DISCUSSION

4.1. Sensitivity Analysis

A comparison of factors across species abundances showed there were different groups of influential factors among the three species (Table 3). Among the influential factors for sea turtle eggs were the interaction coefficients that dealt with the effect of sea turtle eggs on ghost crabs a_{21}, the effect of sea turtle eggs on itself a_{11}, and the effect of raccoons on ghost crabs a_{23}. One aim of this study was to determine the influence of facilitation of raccoons by ghost crabs in this system, and how this affects sea turtle egg abundance and drives the system. In this model, changes in facilitation f had a lower effect on sea turtle egg abundance than other parameters. The interaction coefficient a_{21} represented the effect of sea turtle eggs on ghost crabs and had the highest sensitivity index value and was the main driver of the system. This suggests that the interaction between sea turtle eggs and ghost crabs can have a large impact on this food web. This parameter is interpreted as the effect of the addition of a single sea turtle egg on the per capita ghost crab growth rate. This raises the question: how does sea turtle egg energy enhance ghost crab reproduction? In an intensive field experiment in the Cape Verde archipelago, ghost crabs depredated an average of 50% of the total number of loggerhead eggs (Marco et al. 2015).

The top three influential factors for ghost crab abundance were the interaction coefficients that dealt with the effect of ghost crabs on sea turtle eggs a_{12}, the effect of ghost crabs on itself a_{22}, and the effect of sea turtle eggs on ghost crabs a_{21}. Interactions with sea turtle eggs were important and were an influential source of variation for ghost crab abundance. Interaction parameter a_{12} is interpreted as losses to sea turtle eggs due to ghost crab depredation.

Interaction parameter a_{22} is interpreted as losses to ghost crab abundance due to intraspecific effects such as competition for space or resources. Interaction parameter a_{21} is interpreted as growth for ghost crabs due to direct predation and was also influential for sea turtle egg abundance. Changes in the proportion of facilitation f by ghost crabs to raccoons had a large direct impact on ghost crab abundance, in the model (Table 3).

The top three influential factors for raccoon abundance were the interaction coefficient that represented the effect of raccoons on itself a_{33}, the secondary nest depredation proportion d, and the interaction coefficient that represented the effect of sea turtle eggs on itself a_{11}.

4.2. System Dynamics

In the model, a combination of low facilitation and high depredation levels led to community stability (Figure 10b). High facilitation and low depredation led to community instability and lower diversity (Figure 10b) as one or more species would go extinct. There is a tradeoff between the negative effect of secondary depredation on the resource versus the positive effect (benefit) of facilitation on the consumer. If the consumer does not benefit much (low f), but the resource is significantly harmed (high d), there is stability. Vice-versa, if the consumer benefits much (high f), but the resource is not significantly harmed (low d), there is instability. This could mean that as ghost crabs dig more burrows, raccoons are provided greater access to sea turtle nests leading to community instability.

This system is an example of where increased facilitation leads to community instability. Facilitation in an ecological context has been documented extensively in plant communities (Brooker et al. 2008) and does not always lead to community instability. For example, a similar case study indicates that *Spartina alterniflora* facilitates the establishment and persistence of cobble beach plant communities by stabilizing the substrate and enabling seedlings to emerge and survive (Bruno 2000). However, facilitated predation may not function in the same way as simple facilitation and should be studied further in the future.

This model is an extension of basic intraguild predation models (Polis and Holt 1989; Polis and Holt 1992; Polis and Holt 1997; Diehl and Feibel 2000) for exploration of the impacts of facilitated predation on resource abundances. I showed that a unidirectional facilitative relationship between the prey and consumer had a small effect on resource abundance (Figure 3) and does not promote a stable coexistence (Figure 10) in this system with the estimated parameter values used. A similar intraguild predation modeling study looked at the unidirectional facilitative relationship between the consumer and prey and found that facilitation produced a stable coexistence of both predators and led to three-species coexistence (Shchekinova et al. 2014). Another similar intraguild predation microcosm study involving micro-zooplankton in which the consumer facilitates the prey showed that facilitation increased exploitation of a common resource and opens the possibility for a stable coexistence (Loder et al. 2014).

4.3. Potential Management Considerations

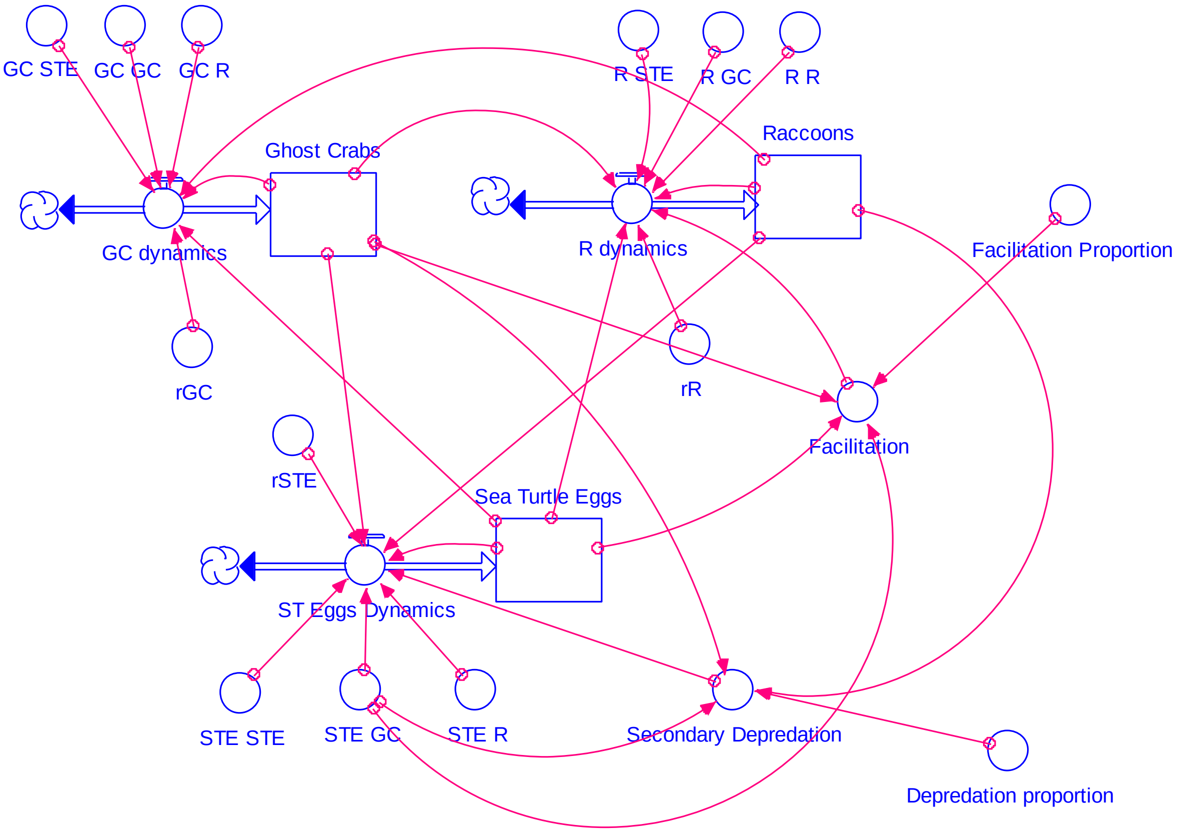
Many studies have focused on sea turtle conservation (Frazer 1992; Hamann 2010; McClenachan et al. 2006). Crouse et al. (1987) suggested that the key to improving the outlook for loggerhead turtle populations is to reduce mortality in later life stages especially the large juveniles based on Southeastern United States loggerhead fecundity, survival and growth rate data. Although this would be ideal, the majority of sea turtle work is conducted on nesting beaches and was the focus of this study. Based on the sensitivity analysis and control scenarios, there are some management implications that can be considered if maximizing sea turtle survivorship is a management goal. It should be acknowledged that there are caveats in the model. For example the model does do something unexpected (the raccoon population skyrockets) which is not representative of the actual system and occurs when certain parameter values are used (Figure 7). However, my results suggest that the system could be more complex than expected and perhaps controlling only for raccoons may be inadequate. The possibility for controlling for ghost crabs should be explored as a management strategy to maximize sea turtle nest production. It may be beneficial if management resources are limited to ignore raccoons and focus on excluding ghost crabs from nests. High levels of ghost crabs have a more significant impact on sea turtle eggs than high levels of raccoons when Figures 11c and 12c are compared. This is supported by Barton and Roth (2008) where the highest rates of egg predation by both predators (31%) occurred when raccoon abundance was lowest and ghost crab abundance was highest in a Central East-Coast Florida beach study. Also, parameters a_{21}, a_{23} and a_{12} involved ghost crabs interacting with sea turtle eggs and were ranked as influential in the sensitivity analysis. A review of sea turtle hatchling production from Florida beaches between the years 2002-2012 revealed that ghost crab depredation was more frequent than mammalian depredation in all but Southwestern Florida and suggested that mortality from ghost crabs should be more closely examined (Brost et al. 2015). If exclusion devices are used (e.g., wire mesh cages) on sea turtle nesting beaches, a smaller mesh cage hole size may prevent ghost crabs from entering nests. This method would be simple to implement and be relatively inexpensive.

Based on the sensitivity analysis, sea turtle nest secondary depredation proportionality *d* was an influential factor affecting sea turtle egg abundance. The facilitation proportionality *f* was also an influential factor affecting sea turtle egg abundance. This means that interactions between raccoons and ghost crabs are important as these indirectly affect sea turtle egg abundance and should be considered as part of a management plan.

4.4 Conclusions

A global sensitivity analysis such as the one used here can be a valuable tool in identifying influential vs. non-influential parameters in many ecological models (e.g., population, meta-population, habitat, landscape). This then allows one to conduct additional analysis on influential parameters. Food-web interactions are complex and consideration of other biotic factors such as other sea turtle nest predators and abiotic factors such as beach dune environmental characteristics could also be coupled to the model. A local stability analysis could be conducted to determine local model behavior around an equilibrium point This is done by taking partial derivatives of the system around an equilibrium point (or stable focus), producing a Jacobian matrix and then calculating eigenvalues λ_1, λ_2, and λ_3 (Acevedo et al. 2013). Further investigation of facilitation could be looked at in this system and its response to habitat stress gradients such as human-used beaches. Although the analysis of this multispecies system was a case study, using different derived parameter values, this model could also be used as a foundation to study similar interactions in other natural communities. Also, exclusion experiments may be appropriate to further elucidate the complex relationships between the species in this simple, yet complex 3-species model.

APPENDIX A. STELLA MODEL MAP AND EQUATIONS USED DURING MODEL DEVELOPMENT



Ghost_Crabs(t) = Ghost_Crabs(t - dt) + (GC_dynamics) * dt
INIT Ghost_Crabs = 100
GC_dynamics = Ghost_Crabs*(rGC-GC_GC*Ghost_Crabs+GC_STE*Sea_Turtle_Eggs-GC_R*Raccoons)
Raccoons(t) = Raccoons(t - dt) + (R_dynamics) * dt
INIT Raccoons = 10
R_dynamics = Raccoons*(rR-R_R*Raccoons+R_GC*Ghost_Crabs+R_STE*Sea_Turtle_Eggs+Facilitation)
Sea_Turtle_Eggs(t) = Sea_Turtle_Eggs(t - dt) + (ST_Eggs_Dynamics) * dt
INIT Sea_Turtle_Eggs = 10000
ST_Eggs_Dynamics = Sea_Turtle_Eggs*(rSTE-STE_STE*Sea_Turtle_Eggs-STE_GC*Ghost_Crabs-STE_R*Raccoons-Secondary_Depredation)
Depredation_proportion = .001
Facilitation = Facilitation_Proportion*STE_GC*Sea_Turtle_Eggs*Ghost_Crabs
Facilitation_Proportion = .01
GC_GC = .00001
GC_R = 0.00001
GC_STE = 0.000001
R_GC = 0.0000001
R_R = .001

R_STE = 0.0000001
rGC = 0.0001
rR = .00001
rSTE = .05
Secondary_Depredation = Depredation_proportion*STE_GC*Ghost_Crabs*Raccoons
STE_GC = 0.000001
STE_R = .000001
STE_STE = .0000001

APPENDIX B. THE 3-SPECIES FACILITATIVE AND INTRAGUILD PREDATION MODEL USING THE R SOFTWARE THAT WAS USED FOR THE EFAST SENSITIVITY ANALYSIS

```
# The working directory to the folder where input parameter sample files are saved
setwd("E:/R_eFAST_10_10_2014/Samples")

# Creates a list of the directory file strings as an array in csv format
x <- list.files(pattern = ".csv")

# Number of files in directory
nfiles <- length(x)

# Zero array that will hold model output values
spp <-0
############
sp <- 0
xp <- array(0,c(2340,3))
for (i in 1:3){
for (j in 1:12){
for (k in 1:65) {
sp <- sp +1
xp[sp,] <- c(i,j,k)}}}
#############

# Outer loop that reads in each csv file
for (y in (1:nfiles)){

    # Stores csv file data
    dataSet <- read.csv(x[y])

    # dataSet dimensions
    d <- dim(dataSet)

    # Inner loop that reads in one row at a time from a particular csv file
    for (i in 1:d[1]){

        # dataSet row values that will be used as input parameter values for the model
        p <- dataSet[i,]

        # Constant parameters not used in the analysis
        r1=0.05
        r2=0.0001
        r3=0.00001

        # Initial conditions
        X <- c(x1=10000,x2=100,x3=10)
```

```
        # Defines the ordinary differential equation model
        lotka3sp <- function(t,X,p)
        {with(as.list(c(X,p)),
        {
          dx1 <- (r1 - a11*x1 - a12*x2 - a13*x3 - dep*a12*x2*x3)*x1
          dx2 <- (r2 - a22*x2 + a21*x1 - a23*x3)*x2
          dx3 <- (r3 - a33*x3 + a31*x1 + a32*x2 + fac*a12*x2*x1)*x3
          list(c(dx1,dx2,dx3))
        })}

        # Model time span and time step
        times <- seq(0,200,by=0.1)

        # Import the differential equation solver package
        library(deSolve)

        # Stores differential equation model output
        t.X <- ode(y=X, times=times, func=lotka3sp, parms=p)

        # Omits time column
        A <- matrix(c(t.X[,2],t.X[,3],t.X[,4]), nrow=2001, ncol=3)

        # Adds column names
        colnames(A) <- c('x1','x2','x3')

        #Print(xp)
        spp <- spp+1
        print(spp)

         # Creates output file directory
          output_file <-
          paste("E:/R_eFAST_10_10_2014/Simulation_Results/",toString(xp[spp,1]),"/",toString(x
          p[spp,2 ]),"/", toString(xp[spp,3]),"/1","/Results.csv",sep = "")

        # Saves output file directory
        write.csv(A, file = output_file,row.names=FALSE)

    }
}
```

REFERENCES

Abrams, P.A. and J.D. Roth. 1994. The effects of enrichment of three-species food chains with nonlinear functional responses. Ecology. 75(4): 1118-1130

Acevedo, M.F. 2013. Simulation of Ecological and Environmental Models. 464 pp. CRC Press.

Alden, K., Read, M., Andrews, P., Timmis, J., Veiga-Fernandes, H. and M. Coles. 2014. spartan: Spartan (Simulation Parameter Analysis R Toolkit ApplicatioN). R package version 2.1. http://CRAN.R-project.org/package=spartan

Allen C.R., Forys, E.A., Rice, K.G., Wojcik, D.P. 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatching turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. Florida Entomologist. 84(2): 250-253

Barton, B.T. 2005. Cascading effects of predator removal on the ecology of sea turtle nesting beaches. M.S. Thesis.

Barton, B.T. and J.D. Roth. 2007. Raccoon removal on sea turtle nesting beaches. Journal of Wildlife Management. 71(4): 1234-1237

Barton, B.T. and J.D. Roth. 2008. Implications of intraguild predation for sea turtle nest protection. Biological Conservation. 141(8): 2139-2145

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology. 96: 18-34

Brown, J.R. 2009. Factors affecting predation of marine turtle eggs by raccoons and ghost crabs on Canaveral National Seashore, FL. M.S. Thesis.

Bruno, J.F. 2008. Facilitation of cobble beach plant communities through habitat modification by Spartina alterniflora. Ecology. 81(5): 1179-1192

Callaway, R.M. 2007. Positive interactions and interdependence in plant communities. Springer. Dordrecht.

Ciric, C., Ciffroy, P. and S. Charles. 2012. Use of a sensitivity analysis to identify influential and non-influential parameters within an aquatic ecosystem model. Ecological Modelling. 246(10): 119-130

Cloutier, C. 1997. Facilitated predation through interaction between life stages in the stinkbug predator *Perillus bioculatus* (Hemiptera: Pentatomidae). Journal of lnsect Behavior. 10(4): 581-598

Cornell, H.V. and J. H Lawton. 1992. Species interactions, local and regional processes, and limits to the Richness of ecological communities: A theoretical perspective. Journal of Animal Ecology. 61(1): 1-12

Crouse, D.T., Crowder, L.B., & H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology. 68(5): 1412-1423

Diehl, S. and M. Feibel. 2000. Effects of enrichment on three-level food chains with omnivory. American Naturalist. 155: 200-218

Dodd, C.K., Jr. 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). U.S. Fish and Wildlife Service, Biological Report. 88(14). 110 pages.

Engeman, R.M., Martin, R.E., Smith, H.T., Woolard, J., Crady, C.K., Shwiff, S.A., Constantin, B., Stahl, M. and J. Griner. 2005. Dramatic reduction in predation on sea turtle nests through improved predator monitoring and management. The Oryx. 39: 318-326

Frazer, N.B. 1992. Sea Turtle Conservation and Halfway Technology*. Conservation Biology 6(2): 179-184

FWC. "2013 Statewide Nesting Totals." Statewide Nesting Totals. N.p., n.d. Web. 11 Dec. 2014. http://myfwc.com/research/wildlife/sea-turtles/nesting/statewide/

Fodrie, F.J., Kenworthy, M.D., and S.P. Powers. 2008. Unintended Facilitation between Marine Consumers Generates Enhanced Mortality for Their Shared Prey. Ecology. 89(12): 3268-3274

Gilpin, M.E. 1979. Spiral chaos in a predator-prey model. The American Naturalist. 113(2): 306-308

Goldberg, D.E. and A.M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. The American Naturalist. 139(4): 771-801

Gurevitch, J., Morrow, L.L., Wallace, A. and J.S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Naturalist. 140(4): 539-572

Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K., Barata, P.C.R., Bjorndal, K.A., Bolten, B., Broderick, A.C., Campbell, L.M., Carreras, C., Casale, P., Chaloupka, M., Chan, S.K.F., Coyne, M.S., Crowder, L.B., Diez, C.E., Dutton, P.H., Epperly, S.P., FitzSimmons, N.N., Formia, A., Girondot, M., Hays, G.C., Cheng, I.J., Kaska, Y., Lewison, R., Mortimer, J.A., Nichols, W.J., Reina, R.D., Shanker, K., Spotila, J.R., Tomás, J., Wallace, B.P., Work, T.M., Zbinden, J., & B.J. Godley. 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. Endangered Species Research. 11: 245-269

Hannan, L.B., Roth, J.D., Ehrhart, L.M., and J.F. Weishampel. 2007. Dune vegetation fertilization by nesting sea turtles. Ecology. 88(4): 1053–1058

He, Q., Bertness, M.D. and A.H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters. 16(5): 695-706. DOI: 10.1111/ele.12080

Holt, R.D. and G.R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: Theoretical perspectives. Ecology. 88(11): 2706-2712

Holt, R.D. and G.A. Polis. 1997. A theoretical framework for intraguild predation. The American Naturalist. 149(4): 745-764

Huxel, G.R. 2007. Antagonistic and synergistic interactions among predators. Bulletin of Mathematical Biology. 69(6): 2093-2104

IUCN. IUCN Red List of Threatened Species. Version 2012.2. Web. 17 Dec. 2012. <www.iucnredlist.org>

Jones, C.G., Lawton, J.H. and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos. 69(3): 373-386

Levins, R. 1968. Evolution in changing environments. Princeton University Press. Princeton, N.J. 120 pp.

Löder, M.G.J., Boersma, M., Kraberg, A.C., Aberle-Malzahn, N. and K.H. Wiltshire. 2014. Microbial predators promote their competitors: commensalism within an intra-guild predation system in microzooplankton. ESA Ecosphere. 5(10): 128. doi: 10.1890/ES14-00037.1

Losey, J.E., and R.F. Denno. 1998. Positive predator-predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. Ecology. 79(6): 2143-2152

Marco, A., da Graça, J., García-Cerdá, R., Abella, E. and R. Freitas. 2015. Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. Journal of Experimental Marine Biology and Ecology. 468: 74-82. doi:10.1016/j.jembe.2015.03.010

Marino S., Hogue I.B., Ray C.J. and D.E. Kirshner. 2008. A methodology for performing global uncertainty and sensitivity analysis in systems biology. Journel of Theoritical Biology. 254(1): 178-196

McClenachan, L., Jackson, J.B., & Newman, M.J. 2006. Conservation implications of historic sea turtle nesting beach loss. Frontiers in Ecology and the Environment. 4(6): 290-296

McMurtray, J. 1986. Reduction of raccoon prédation on sea turtle nests at Canaveral National Seashore, Florida. Thesis. University of Georgia. Athens, USA.

Meyer, J.J. and J.E. Byers. 2005. As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam. Ecology Letters. 8: 160-166

Miller, J.D., Limpus, C.J., Godfrey, M.H. 2003. "Nest site selection, oviposition, eggs, development, hatching and emergence of loggerhead turtles". In Bolten, A. and B. Witherington. Loggerhead Turtles. Smithsonian Books. 125–143. ISBN 1588341364. February 28, 2013.

Morrow, K., Bell, S.S., and A. Tewfik. 2014. Variation in ghost crab trophic links on sandy beaches. Marine Ecology Progress Series. 502: 197-206

Morin, P.J. 1999. Community Ecology. Cambridge University Press. Cambridge.

National Marine Fisheries Service and U.S. Fish and Wildlife Service. 2008. Recovery plan for the Northwest Atlantic population of the loggerhead sea turtle (*Caretta caretta*), Second Revision. National Marine Fisheries Service. Silver Spring. Maryland, USA.

Oviedo, R., Faife-Cabrera, M., Noa-Monzón, A., Arroyo, J., Valiente-Banuet, A. and M. Verdú. 2013. Facilitation allows plant coexistence in Cuban serpentine soils. Plant Biology. 16(4): 711–716. DOI: 10.1111/plb.12116

Polis, G.A., Myer, C.A. and R.D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecological Systems. 20: 297-330

Polis, G.A. and R.D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution. 7: 151-155

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Saltelli A., Tarantola S. and K.P.S. Chan. 1999. A quantitative model-independent method for global sensitivity analysis of model output. Technometrics. 41(1): 39-56

Saloranta, T.M., Andersen T. and K. Naes. 2006. Flows of dioxins and furans in coastal food webs: Inverse modeling, sensitivity analysis, and applications of linear system theory. Envioronmental Toxicology and Chemistry. 25(1): 253-264. DOI: 10.1897/05-091R.1

Saltelli A., Chan K. and Scott E.M. 2000. Sensitivity Analysis. John Wiley.

Shchekinova, E.Y., Löder, M.G.J., Boersma, M. and K.H. Wiltshire. 2014. Facilitation of intraguild prey by its intraguild predator in a three-species Lotka–Volterra model. Theoretical Population Biology. 92: 55–61

Soetaert, K., Thomas Petzoldt, R. Woodrow Setzer (2010): Solving differential equations in R: Package deSolve. Journal of Statistical Software. 33(9): 1-25. http://www.jstatsoft.org/v33/i09/

Soliveres, S., Smit, C. and F.T. Maestre. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. 90(1): 297-313. DOI: 10.1111/brv.12110

Sih, A., Crowley, P., McPeek, M., Petranka J. and K. Strohmeier. 1985. Predation, competition, and prey communities: A review of field experiments. Annual Review of Ecology and Systematics. 16: 269-311

Stewart, K., and C. Johnson. 2006. *Dermochelys coriacea*-leatherback sea turtle in P.A. Meylan,editor. Biology and conservation of Florida turtles. Chelonian Research Monographs. 3:144-157

Upadhyay, R.K. and S.N. Raw. 2011. Complex dynamics of a three species food-chain model with Holling type IV functional response. Nonlinear Analysis: Modelling and Control. 16(3): 353–374

Vance, R.R. 1978. Predation and resource partitioning in one predator-two prey model community. The American Naturalist. 112:797-813

Wand, M.P. 2009. gplots. URL http://www.R-project.org/.

Witherington, B. E. and L. M. Ehrhart 1989a. Status and reproductive characteristics of green turtles (*Chelonia mydas*) nesting in Florida. Pages 35 1-352 in L. Ogren, F. Berry, K. Bjorndal, H. Kumpf, R. Mast, G. Medina, H. Reichart and R. Witham (eds.), Proceedings of the second Western Atlantic turtle symposium. NOAA Tech. Memo. NMFS-SEFC-226,401 pp.

Welicky, R.L. et al. 2012. A retrospective analysis of sea turtle nest depredation patterns. The Journal of Wildlife Management 76(2): 278-284