

INFLUENCE OF FOOD WEB STRUCTURE
ON PREDATOR-PREY DYNAMICS
IN A PATCHY ENVIRONMENT

by

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Influence of Food Web Structure on Predator-Prey Dynamics in a Patchy Environment

Thesis directed by Assistant Professor Samuel M. Flaxman

In order to model the spatial distributions of predators and prey many investigators have used a simplified three-species system where a predator species consumes a prey species that consumes a resource. One of the recurring predictions from such models is that the spatial distribution of the predator will match the spatial distribution of the resource instead of that of the prey; this is known as “leapfrogging”. While it is interesting that leapfrogging is consistently predicted by models of three species, tritrophic systems, real biological communities are more complicated, being less like chains and more like multi-dimensional food webs (i.e., multiple prey and predator species interacting with each other). I ask: Are systems with more species and more connections among them well approximated by simpler, three-species single-chain models? I construct two different five-dimensional systems (a resource consumed by two prey species consumed by two predator species) and compare them to the single-chain system to see if more complicated systems yield the same predictions as a simpler single-chain system. I discovered that, in aggregate, the dynamics of predators in a multi-species web, is very similar to the dynamics of a simpler, single-chain system; yet individually the dynamics of predator species in a multi-species web are very different from the dynamics of a simpler, single-chain system.

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1 Introduction

Extensive research has explored spatial distributions of organisms in patchy environments. At small spatial scales, Fretwell and Lucas’s [12] Ideal Free Distribution has provided a theoretical basis for predicting spatial distributions. Basic ideal free distribution models assume that individual animals are “ideal” in that they have complete information about patches of habitat, and are “free” from any costs to move from one patch to the next. With these assumptions, foragers are predicted to move among patches of habitat until per capita gains from foraging are equal across all patches. A distribution satisfying this condition is called an “ideal free distribution” (henceforth, “IFD”) [12, 17]. IFD models with a wide variety of forms of resource variation and competition have been reviewed by Schwinning and Rosenzweig [24] as well as Whitman and Mathis [28], and can indeed predict the distribution of foragers in different patches.

A number of researchers [1, 3, 11, 12, 14, 15, 20, 24] have also studied whether IFDs would be reached in different multi-species models, under various assumptions about movement and information gathering abilities. The results of these studies are quite varied with respect to predictions about whether or not IFDs would be reached by one or more species involved, or if the multi-species systems even have an equilibrium. Hence, much current research, both empirical and theoretical, is aimed at providing better understanding of multi-species habitat selection games.

The most commonly examined multi-species IFD models considered are three species “single-chain” systems (e.g. predator - herbivore - plant) [3, 11, 12, 14, 15, 24]. A number of previous models—focused on optimal, equilibrium distributions—predict that predators in a single-chain system will display a “leapfrog” effect in which their spatial distribution more closely matches that of the prey’s resource (which the predators do not consume) than that of the prey [11, 13]. This leapfrog effect is counterintuitive and qualitatively different from the predictions of models that only consider two trophic levels (i.e herbivore - resource), which generally predict that there will be a close correspondence between the consumer and the resource it eats [18]. This counterintuitive prediction (i.e., predators superficially appearing

to ignore the distribution of their prey) arises from the fact that a single-chain system can only reach an equilibrium when the distribution of predators is such that predation offsets prey births. Thus, predators must concentrate where prey have the highest birth rates (i.e., where resources that the prey consume are most abundant; see also [11, 23, 25] for additional explanations).

Although this leapfrogging distribution is predicted by many three species single-chain models (reviewed in [23, 25]), when another trophic level is added (e.g. Top predator - Intermediate predator - Herbivore - Plant) the leapfrog effect is altered [22, 23, 29, 30]. With four trophic levels, Rosenheim [23] found instead that the top predator aggregated strongly where the resource is most abundant which prevented the intermediate predator from aggregating strongly where the resource is most abundant, and again allowed the herbivore to aggregate more strongly where the resource is most abundant [23]. In a single-chain systems with 4 species it is the top predator who offsets the birth rates, and so the top predator concentrates where the resource is most abundant [23].

Each of the systems that have been studied could be argued to be over simplified. In nearly all empirical systems, a single species each of predator, prey and resource are not the only ones present. Rather, prey may face threats from more than one predator, predators might be able to consume more than one species of prey, and predators or prey may face competition from different species on the same level as them. Hence, while the leapfrog effect has been considered to be a general, robust prediction about spatial distributions, the addition of more biological realism raises questions about the kinds of distributions we should actually expect in nature, and whether the distributions predicted by simple models (single-chain or simpler) should be observed in real systems.

These questions have begun to be studied by different researchers [4, 5, 7, 8]. Abrams [4, 5] has studied how the spatial distributions of prey change when there is intraguild predation among predators. Intraguild predation is predation between two species on the same trophic level (i.e. two predators who not only consume prey but one predator can also consume the other). Abrams predicted that prey abundances would increase in patches with enriched resources when intraguild predation of the predators was present, showing how

the addition of biological realism may lead to important qualitative changes about predicted distributions of organisms. While Abrams focused on how prey abundances would be affected by intraguild predation he does discuss predator distributions to a certain extent as well. In his paper [4], the spatial distributions of the predators seem to act more similarly to those in the four trophic system studies by Rosenheim [23] than other tri-trophic systems. This leads me to believe that predators individually may not be leapfrogging, although since Abrams was focused on prey distribution, he does not talk about this in his paper.

Amarasekare [7, 8] studied more complex food web systems, focusing on what kinds of movement dynamics would lead to the co-existence of all species in more complex food webs. While she does not specifically study leapfrogging or spatial distributions of prey and predators, her work with movement dynamics outlines more of the differences between complex food webs and simple tri-trophic systems. We continue to see in these papers that the spatial distribution of predators and prey can be altered by the complexity of the food web. It is clear from these papers that adding another predator or prey, and adding intraguild predations can alter predictions about the spatial distribution of predators.

Biological communities in nature are generally not linear food chains but are much more like large, highly connected networks (i.e., food webs) [7, 8, 19, 20, 26, 29, 30]. Are there general, robust predictions—leapfrogging or otherwise—that can be derived about the spatial distribution of predators and prey from models with more realistic structure than a simple three-species chain? The goal of this thesis is to investigate how different added dimensions of competition for prey and predators to the usual tri-trophic system will affect the leapfrogging prediction among predator species. This will allow us to further understand whether simple tri-trophic models are likely to be able to correctly predict the spatial distribution of predators in more realistic situations. This thesis will show that under specific movement strategies individual predator species will no longer undergo the leapfrog effect in complex food web systems, but that the aggregate of predator species in a patch do, in general, undergo the leapfrog effect.

2 Methods

To better understand whether predictions from simpler models may apply to more highly connected networks, I have considered two different food web systems in addition to the single-chain system which will be used as the base model (Figure 1a). The first food web is a “two-chain” model (Figure 1b): it consists of two predators, two herbivores and a single plant resource. In this system, the two species of herbivores both eat a single plant resource, and each species of predator eats one herbivore but not the other herbivore (i.e., the two predator species do not share the same prey). This system’s purpose is to see how two different predators and prey species co-exist in the same patches when the prey compete with each other but the predators do not directly compete.

In the second, five-species system, there are again two predators, two herbivores and a single plant resource (Figure 1c). The herbivores both eat the plant resource, but this time each predator can eat both of the herbivores. This system’s purpose is to see how predators distribute themselves when they are competing with another species on their level.

In sum, I consider three models: (1) a “single-chain” model of three species in a tri-trophic arrangement (Figure 1a), (2) a “two-chain” model with five species, in which the two tri-trophic chains have a common base resource (Figure 1b), and (3) a “web” model with five species and multiple connections between them (Figure 1c).

Table 1: Definitions of variables used in the models

<i>Symbols</i>	<i>Meaning</i>
R_i	resource abundance in patch i
$N_i, N_{i,j}$	abundance of prey in patch i ($= 1$ or 2 , single-chain model); abundance of prey species j ($= A$ or B) in patch i (models with 5 species)
$P_i, P_{i,l}$	abundance of predator in patch i (chain model); abundance of predator species l ($= X$ or Y) in patch i (models with 5 species)
a_i	resource growth rate in patch i
K	carrying capacity of the resource
α, α_j	consumption rate of the resource by the prey; consumption rate of the resource by the prey species j
r, r_j	growth rate of prey; growth rate of prey species j
$b, b_{j,l}$	consumption rate of the prey by the predator; consumption rate of prey species j by predator species l
k, k_l	intrinsic death rate of the predator; intrinsic death rate of predator species l
$c, c_{j,l}$	growth rate of the predator; growth rate of predator species l due to consumption of prey species j

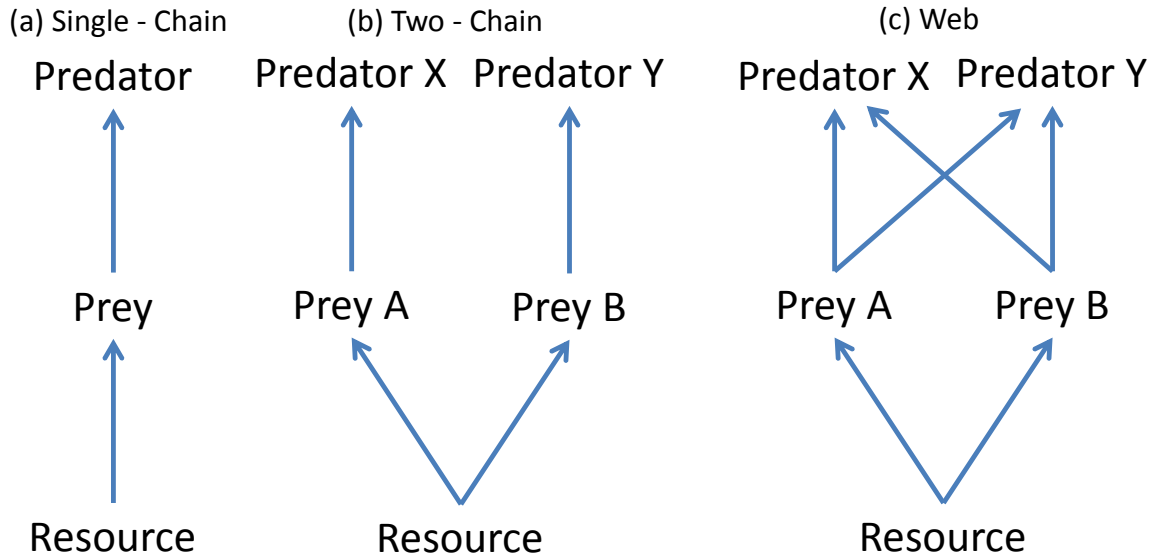


Figure 1: Representations of the three different models considered. Each arrow points from a food source to a species that consumes it.

For the scope of this thesis I will consider modeling resource growth logistically [9, 15], while having exponential growth of all other species. Since the resource is being modeled logistically the prey and predators can not grow infinitely, as they are limited by the abundance of the resource. Standard functional forms for birth and death processes [8, 9, 21, 15, 27]

were used to model these dynamics with systems of ordinary differential equations, which, for three species, take the following form:

$$\dot{R}_i = a_i(1 - \frac{R_i}{K})R_i - \alpha R_i N_i \quad (1)$$

$$\dot{N}_i = r R_i N_i - b N_i P_i \quad (2)$$

$$\dot{P}_i = c N_i P_i - k P_i \quad (3)$$

where R_i, N_i, P_i are the abundances of resources, prey, and predators (respectively) in patch i ($= 1 \text{ or } 2$) at time t , and \dot{R}_i, \dot{N}_i , and \dot{P}_i are the rates of change in these abundances. a_i is the intrinsic growth rate of the resource in patch i , K is the carrying capacity of the resource, α is the consumption rate of the resource by prey, r is the intrinsic growth rate of the prey, b is the consumption rate of the prey by the predator, $c(< b)$ is the growth rate of the predator (due to consumption of prey), and k is the intrinsic rate of death of predators. Note that here and elsewhere, a_i is the only source of between-patch heterogeneity that is built into the model (i.e., I assume $a_1 \neq a_2$).

For the five-species systems, these equations become:

$$\dot{R}_i = a_i(1 - \frac{R_i}{K_i})R_i - \alpha_A R_i N_{i,A} - \alpha_B R_i N_{i,B} \quad (4)$$

$$\dot{N}_{i,j} = r_j R_i N_{i,j} - b_{j,X} N_{i,j} P_{i,X} - b_{j,Y} N_{i,j} P_{i,Y} \quad (5)$$

$$\dot{P}_{i,l} = c_{A,l} N_{i,A} P_{i,l} + c_{B,l} N_{i,B} P_{i,l} - k_l P_{i,l} \quad (6)$$

where variables have the same meanings as in equations (1)-(3), but subscripts are added as needed to incorporate two species of prey and two species of predators (see Table 1). Specifically, I represent prey species j ($= A$ or B) by abundance $N_{i,j}$ in patch i at time t . Likewise, I represent predator species l ($= X$ or Y) by abundance $P_{i,l}$ in patch i at time t . Consumption and growth parameters also become species-specific: α_j is the consumption

rate of the resource by prey species j , $b_{j,l}$ is the consumption rate of prey species j ($= A$ or B) by predator species l ($= X$ or Y), and $c_{j,l}(< b_{j,l})$ is the growth rate of predator species l from consumption of prey species j . Note that for the “two-chain” model (Figure 1b), each predator consumes only one species of prey, and thus in equations 5 and 6, $b_{A,Y} = b_{B,X} = c_{A,Y} = c_{B,X} = 0$. In the “web” model (Figure 1c) we instead have $b_{A,Y}, b_{B,X}, c_{A,Y}, c_{B,X} > 0$, reflecting the fact that both species of predator consume both species of prey.

Multiple types of movement dynamics for foragers and predators in have been discussed [2, 6, 16]. No specific movement dynamic has been found to be the best strategy for every situation, although much of previous research has modeled random movement alone or in combination with some linearly conditional movement term(s). I considered conditional movement strategies that were discussed in the review paper by Krivan et al. [16] as well as those discussed by Abrams [2, 6, 16] and used in some of his investigation of complex food webs. For animals engaged in habitat selection behavior, conditional movement strategies are generally regarded as being more realistic than random movement (or no movement) [1, 2, 6, 8, 16]. Note that, “movement” in this context is cost-free, fixed, and may be considered to be “habitat selection”, i.e., small scale movements that a single organism can make many times within its expected lifetime.

The analysis of the three different systems with conditional movement dynamics leads to two different sources of information by which to define the predator and the prey’s movement. These conditional movement dynamics are very similar to those used in previous research done by Flaxman et al. [10, 11]. Specifically, prey’s conditional movement dynamics could be defined by movement toward the patch where the resource was more abundant or where the predators were least abundant. Predators’ conditional movement dynamics could be defined by movement toward where either the prey were most abundant or the resource was most abundant. (Reasons why it might be adaptive for predators to move up the gradient of a resource they do not consume are discussed by Flaxman and Lou [11].) These different movement dynamics gave us a variety of different combinations of prey and predator movement strategies to consider. The most intuitive movement dynamics to use [2, 10], and the one I will focus on here, is when the prey’s conditional movement dynamics are defined

by movement towards the patch where resource was more abundant; and where the predator's conditional movement dynamics could be defined by movement towards where the prey were most abundant. In other words, both species are moving towards where their "food" is more abundant. To model the different systems with these movement dynamics I added corresponding conditional movement terms to the dynamics of each patch. The equations for the resource dynamics are still given by equations 1 and 4 depending on if we are in the three-species or five-species systems, respectively. The equations for the prey and predator species are now modified with the addition of the following conditional movement terms:

For prey movement dependent on resource abundance:

$$-d * \max(0, (R_2 - R_1)/(R_2 + R_1)) * N_{1,j} + d * \max(0, -(R_2 - R_1)/(R_2 + R_1)) * N_{2,j} \quad (7)$$

or

$$+d * \max(0, (R_2 - R_1)/(R_2 + R_1)) * N_{1,j} - d * \max(0, -(R_2 - R_1)/(R_2 + R_1)) * N_{2,j} \quad (8)$$

is added to equation 5 in patch 1 and patch 2 respectively.

For predator movement dependent on prey abundance:

$$-D * \max(0, (N_2 - N_1)/(N_2 + N_1)) * P_{1,l} + D * \max(0, -(N_2 - N_1)/(N_2 + N_1)) * P_{2,l} \quad (9)$$

or

$$+D * \max(0, (N_2 - N_1)/(N_2 + N_1)) * P_{1,l} - D * \max(0, -(N_2 - N_1)/(N_2 + N_1)) * P_{2,l} \quad (10)$$

is added to equation 6 in patch 1 and patch 2 respectively.

Similar movement strategies have been considered and are discussed by Flaxman and colleagues [10, 11] as well as Abrams [2]. These movement strategies have also been discussed by Krivan et al. [16]; where it has been noted that simple linear relationships between predator and prey species, like the ones described in the above movement equations, are some of the more realistic ways of representing predator and prey movement in nature [16]. In equations 7-10, d and D are movement rate parameters, or can also be thought of as the sensitivity parameters, of the prey and predator species, respectively. Larger values of these parameters cause higher movement rates for a given difference between patches. The

max functions found in these equations define information use by the predators or prey. Each function has a normalized difference of the abundances being used for conditional movement. I also note that, with the conditional movement the prey and predators species are only moving in one direction without error.

For the scope of this thesis, I am interested in whether equilibria exist, and if so, if equilibrium abundances of organisms in the two patches are (1) IFDs and (2) exhibit leapfrogging in food webs with various numbers of species and links between them. In order to examine whether they are IFD, the abundances of the predators and prey were compared with abundances that would be expected when predators and prey maximize their fitness by foraging in the highest quality patch (i.e. predators and prey choose to forage in the “ideal” patch). In order to examine whether leapfrogging distributions are predicted at equilibrium, I asked whether predator abundance in a patch was proportional to resource abundance in a patch (not necessarily proportional to prey abundance in the patch). That is, if a leapfrogging distribution occurs at equilibrium, for the single-chain system I should observe that

$$\frac{\hat{P}_1}{\hat{P}_2} = C \frac{\hat{R}_1}{\hat{R}_2} \quad (11)$$

where C is a combination of parameters (constants) from the model, and \hat{P}_i , \hat{R}_i are the equilibrium abundances of predators and resources in patch i respectively. If $C = 1$, we say that the predators undergo perfect resource matching, because the ratio of predators is equivalent to the ratio of resources. If $C \neq 1$ but is still constant over time, we say that the predators undergo resource matching but not perfect resource matching.

3 Results

Since analytical solutions were not possible with conditional movement I used numerical simulations, using MATLAB’s `ode45` routine to explore the dynamics of the three different systems. These simulations were used to verify whether systems would reach an equilibrium and to quantify the degree of departure from perfect resource matching (the value of C) as

parameters of the system were changed. The initial conditions for each system had little to no bearing on the end results of the simulations. Large changes in initial conditions could change the end abundances of prey or predators, but would never change the behavior of the systems. The parameter values assigned to the variables in equations (1) - (6) represent each species' effectiveness at surviving, reproducing or consuming. I explored the equilibria of the system while allowing the birth/growth and consumption/death parameters to vary between 0 and 1, where a value closer to 1 means the species are more efficient at reproducing or consuming (with the exception of the death parameter for the predators where a higher value implies a higher mortality rate). The carrying capacity of the resource was allowed to vary between 20 and 50, maintaining only that one patch had a higher capacity than the other. Since abundance is an arbitrary unit in this thesis, the carrying capacities only purpose is to cap predator and prey abundances. For the scope of this thesis, I only considered regions of parameter space (numerically determined) in which none of the species would go extinct. (While extinction and coexistence are, of course, important questions, they are beyond the scope of the current thesis.) I also have different movement rates for both the predators (D) and the prey(d), which I allowed to vary between 0 and 1 with a step size of 0.1. As was discussed earlier this is to vary the sensitivity of prey and predators to differences between patches, the closer the value is to one the more sensitive the predators and prey are to the information. A value greater than 1 would lead to another growth term for predators or prey, while a value less than 0 would imply that the predators are moving opposite what is ideal. Either one of these cases is unrealistic and so values were only varied between 0 and 1.

Once the parameters were chosen, `ode45` was run until an equilibrium was reached, or a max number of time steps was reached (5000). In this thesis 50 time steps represents the time it takes for one generation of prey to be replaced by a new generation, and 75 time steps represents the time it takes for one generation of predators to be replaced by a new generation. The predator species in the systems that reached an equilibrium were analyzed to see if they were resource matching. In the systems that did not reach an equilibrium, the sum of the predator species was analyzed to see if there was "trophic level" leapfrogging

even if individual species were not showing that pattern. Using this information each of the systems could be compared to one another. I used these analyses to derive predictions about the effects of explicit, conditional movement on dynamics and spatial distributions.

3.1 Single-chain Model

Examining different movement strategies in the single-chain model (figure 1a), the prey and predator abundances always reached an equilibrium. However, when an equilibrium was reached the spatial distributions of the predators and prey were not always IFDs. Figures 2 and 3 show that when the prey are allowed to move the distributions of the predators and prey no longer matched the IFD. In fact, the more sensitive the prey are (i.e. as d gets larger), the farther the predators will be from IFD. Figure 4 shows that the predators only undergo perfect leapfrogging when the prey are not moving.

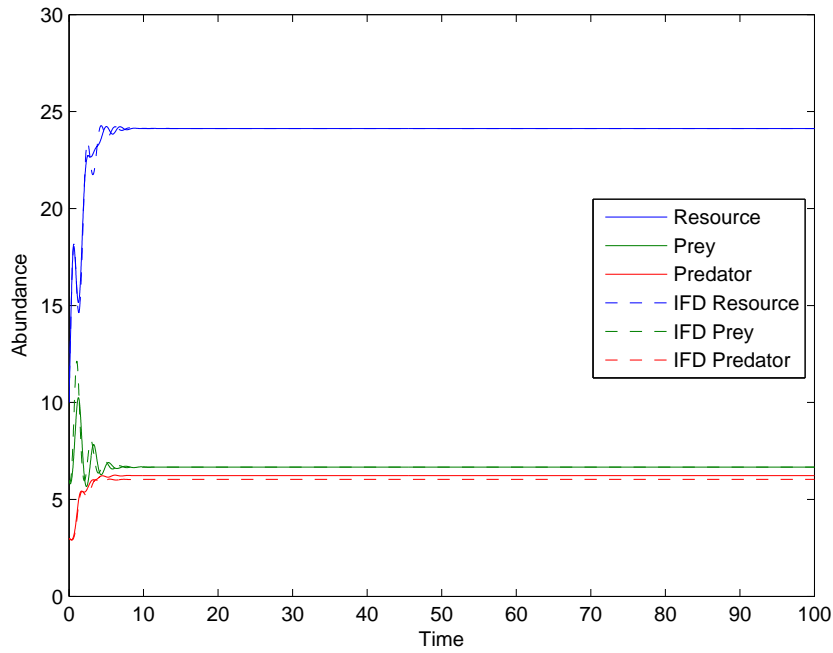


Figure 2: Behavior of the single-chain system when both the prey and predator species are allowed to move. The prey move depending on the resource abundance, the predators move depending on the prey abundance. Parameter values are $a = 4$, $a_2 = 4.2$, $\alpha = .25$, $r = .2$, $b = 1.5$, $c = .15$, $k = 1$, $K = 30$, $K_2 = 40$, $d = .5$, $D = .8$.

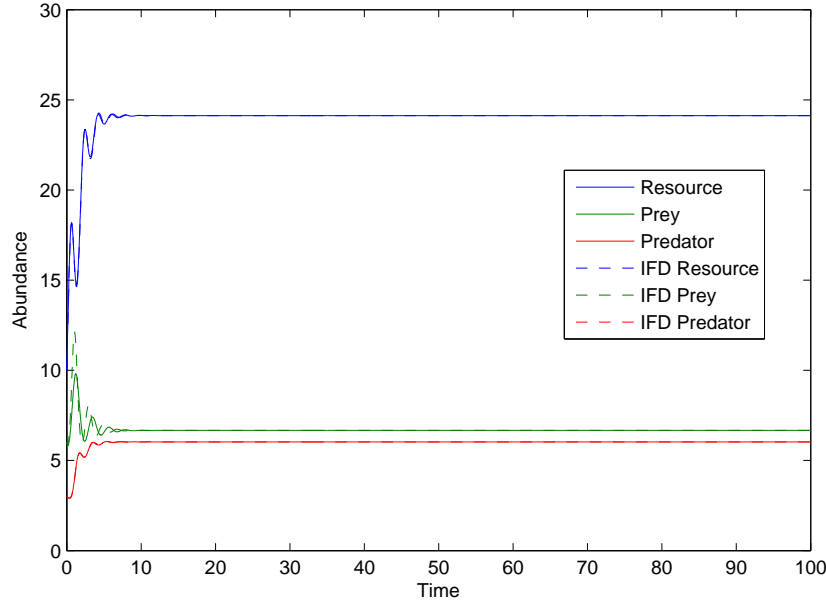


Figure 3: Behavior of the single-chain system when only the predator species are allowed to move. The predators move depending on the prey abundance. Parameter values are $a = 4, a_2 = 4.2, \alpha = .25, r = .2, b = 1.5, c = .15, k = 1, K = 30, K_2 = 40, d = 0, D = .5$.

Figure 4 shows how close the single-chain system is to resource matching (represented by the equilibrium value of C) when D and d are varied from 0 to 1. Note that the value of D does not matter when it comes to the resource matching constant. As was mentioned above I observe that the predators exhibit perfect resource matching ($C = 1$) if the prey are not moving (i.e., whenever $d = 0$). However, as the prey movement rate, d , is increased from zero, the predators get farther and farther away from perfect resource matching, as well as IFD. Specifically, as the prey movement rate increases the predator's resource matching, C , value increases above 1. This means that the predators are overmatching (i.e. there are more predators in the patch with more resources than there would be at the IFD [18]).

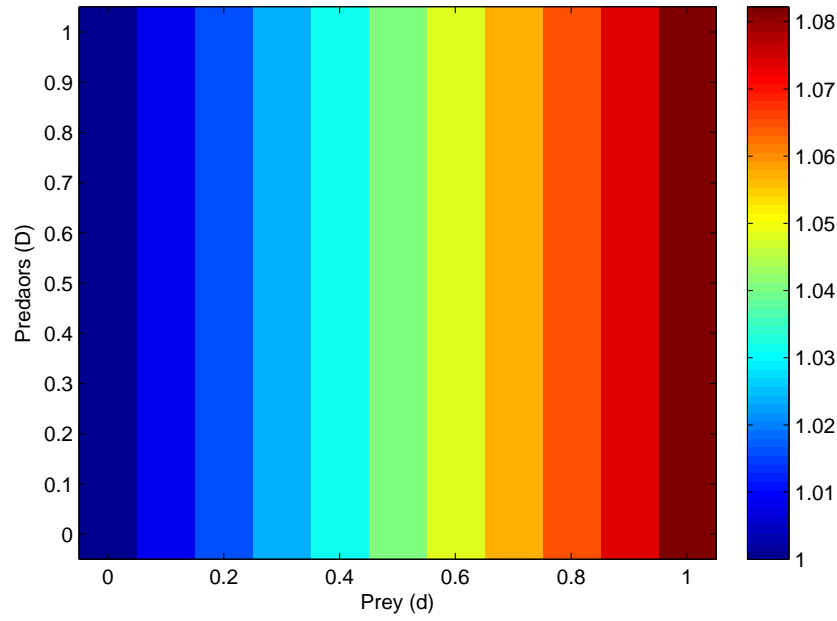


Figure 4: Values of the resource matching constant, C , with D and d varied from 0 (no movement) to 1 in step size of 0.1. Values of $C > 1$, indicate overmatching and departure from IFD by the predators (see text). Parameter values (other than D and d) are as in Figure 2.

3.2 Two-Chain Model

In the two-chain system where there are two different prey species and two different predators species, I first explored whether or not the system reached an equilibrium for the given movement strategy. It was found that reaching an equilibrium was dependent the movement rates (D and d). Figure 6 has a region of black where the system leads to oscillations in the predator and/or prey abundances (i.e., the system did not reach equilibrium). In parameter regions where an equilibrium was reached, I then asked how much or little predators deviated from resource matching, much like I did in the single-chain system.

In this system I examined whether the predator species individually and in aggregate reached IFD and in turn perfect resource matching when the system is in an equilibrium. Figure 5 demonstrates that, as in the single-chain model, the predators will not reach the IFD when the prey have conditional movement. Since I focus on the predators individually as well as in aggregate, there are three sets of results on resource matching (one for predator

species A , one for predator species B , and one for the sum of the predator species).

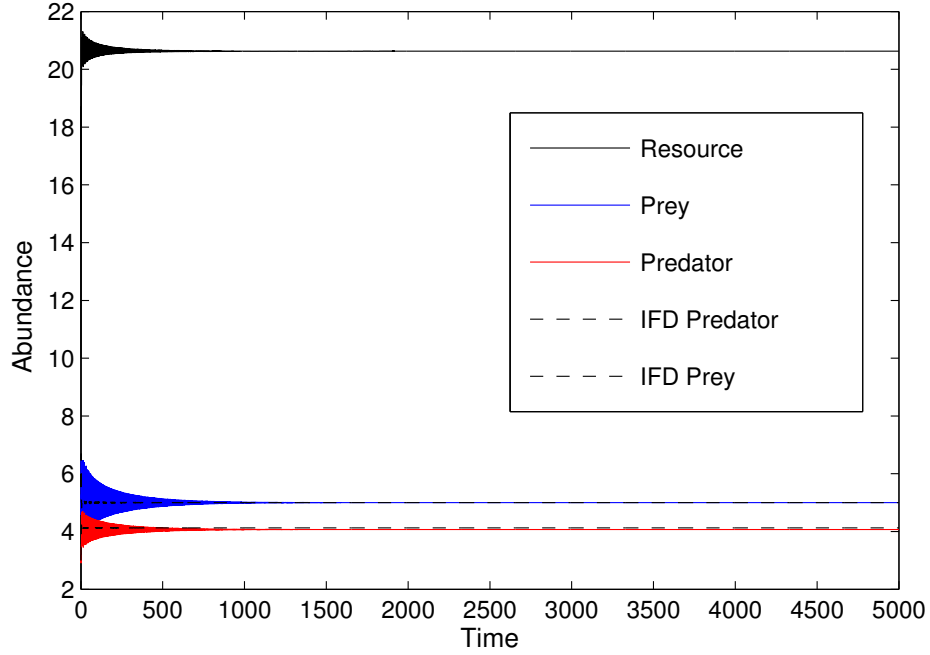


Figure 5: Behavior of the two-chain system when only the predator species are allowed to move. Only one predator and prey species from patch 1 is displayed for clarity. The predators move depending on the prey abundance. Parameter values are $a = 4, a_2 = 4.2, \alpha = .15, \beta = .1, r_1 = .11, r_2 = .1, b_1 = .55, b_2 = .5, c_1 = .11, c_2 = .1, k_1 = .55, k_2 = .5, K = 30, K_2 = 40$.

Figure 6 demonstrates these different sets of results (each panel is for one of the three different cases). Panel (a) displays the degree of resource matching, C , for predator species A , panel (b) displays C for predator species B , and panel (c) displays C for the sum of the predator species. In each of the panels the predators only exhibit perfect resource matching if the prey are not moving ($d = 0$), and as the prey's movement rate, d , increases C increases from 1, indicating overmatching (i.e. the predators are over-aggregated in the best quality patch compared to the IFD). Thus, as was observed in the single-chain model, only when prey do not move do I see both species at an IFD.

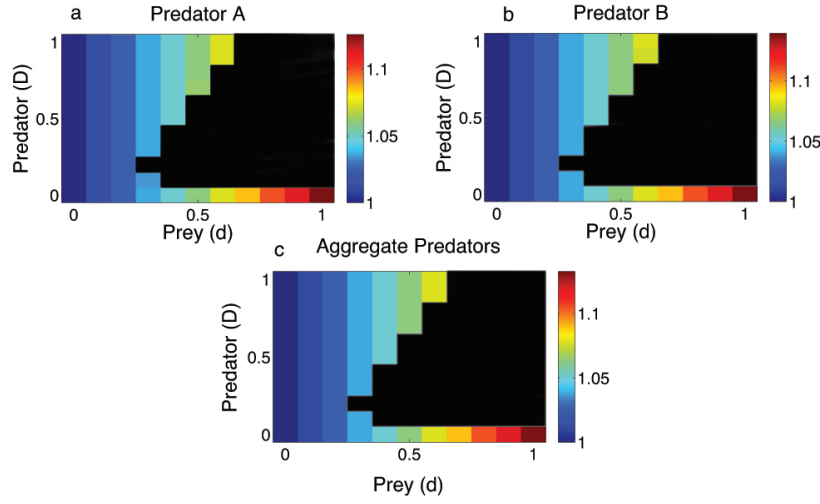


Figure 6: Values of the resource matching constant, C , for predator species (a,b) individually and (c) in aggregate, with D and d varied from 0 (no movement) to 1 in step size of 0.1. (a) The degree of resource matching by predator A . (b) The degree of resource matching by predator B . (c) The degree of resource matching by the sum of the predator species. Interpretations of shading are as in Figure 4, with the exception that black regions represent areas lacking a stable equilibrium. Parameter values are as in figure 5.

3.3 Web Model

The web model consists of two different prey species and two different predator species that are generalists. While the two predator species are to be distinct from one another and generalists, simply making one predator species more adept at consuming and/or reproducing would lead to the extinction of one of the prey species and/or one of the predator species. Instead, I considered two predator species distinguished by the prey that they “preferred”. While both predator species consume both of the prey species (since they are generalists to a certain degree), each predator has higher rates of consumption and reproduction stemming from one of the prey. This in turn also creates a distinction between the two prey species, since they are consumed at different rates from the two different predator species. When considering a web system, as described, where neither predator species has an outright competitive advantage, but instead vary in the consumption rates by each of the prey species, the system will exhibit an oscillatory behavior where all the predator and prey species may exist.

As in the two-chain system, I examined if the predators distribution individually and in

aggregate reached perfect resource matching. Figure 7 demonstrates the oscillatory behavior the web systems will exhibit under the scenario that allows all species to exist. Given that the predators are oscillating, there is no way that individually they can undergo perfect resource matching when the resource is constant. Still, the spatial distribution of the predators in aggregate can be examined, to see if they exhibit perfect resource matching. I discovered that the predators in aggregate will exhibit “leapfrogging” ($C = 1$). Figure 8 displays this constant C for the aggregate predators in the web model. From this figure it can be observed that C is 1 for the aggregate predators regardless of the movement value D and much like the previous two systems only when the prey movement rate is zero ($d = 0$).

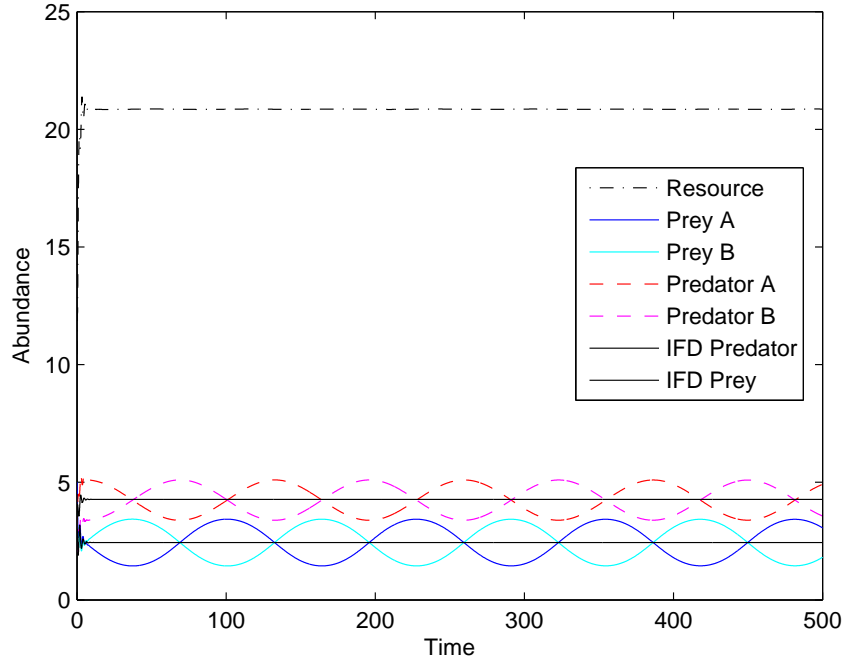


Figure 7: Oscillatory behavior of the predators and prey in one of the patches of the web model. The prey move depending on the resource abundance, the predators move depending on the prey abundance. Parameter values are $a = 4, a_2 = 4.2, \alpha = .25, \beta = .25, r_1 = .21, r_2 = .21, b_1 = .525, b_2 = .525, c_1 = .21, c_2 = .21, k_1 = 1, k_2 = 1, x_1 = .5, x_2 = .5, z_1 = .2, z_2 = .2, K = 30, K_2 = 40, d = .5, D = .8$.

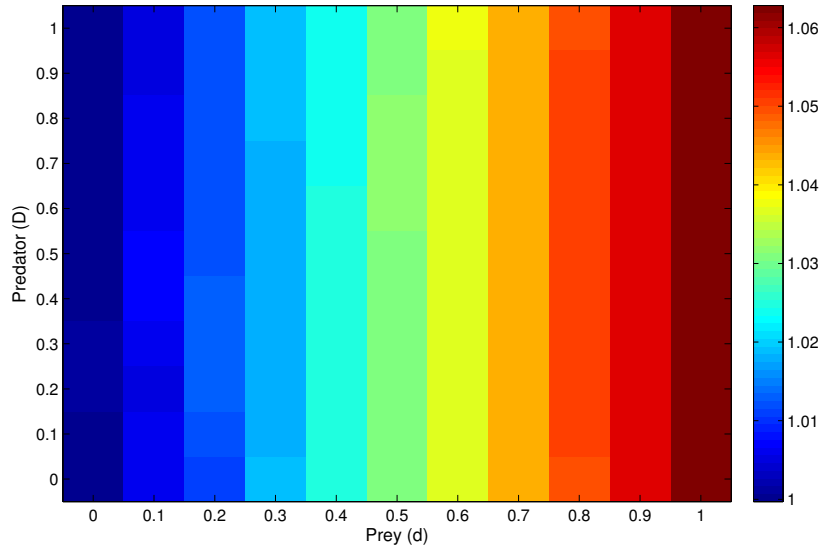


Figure 8: Values of the resource matching constant, C , for predator species in aggregate, with D and d varied from 0 (no movement) to 1 in step size of 0.1. Interpretations of shading are as in Figure 4. Parameter values are as in figure 7.

4 Discussion

Previous research that has explored spatial distributions of predators in three species, “single-chain” systems has predicted that the predator’s spatial distribution (instead of the prey’s) should match the distribution of resources in each patch instead of matching the distribution of the prey which they consume (a phenomenon known as “leapfrogging”) [3, 11, 12, 14, 15]. However, as more complex systems have been studied it has been found that predictions about the spatial distributions of prey do not match those from simpler systems [4, 5]. This casts doubt on the generality of the leapfrogging prediction.

Here I have analyzed two more complex tri-trophic systems: (1) a two-chain system in which an immobile resource is consumed by two different prey species, that are each attacked by a different specialist predator species, and (2) a web system in which an immobile resource is consumed by two different prey species, that are attacked by two different predators that are generalists (i.e. each predator can consume both of the prey species). In each system the predators and the prey were given explicit movement dynamics similar to the linear

movement dynamics discussed by Kriřan et al. [16]. In order to examine the leapfrogging distributions at equilibrium, I asked whether the ratio of predator species' abundances in the two patches was proportional to the ratio of the resource abundance in the two patches (this ratio is the constant referred to as C). For the scope of this thesis, I am interested in the degree to which C deviates from unity, which would mean perfect resource matching and mean that the predator was "leapfrogging".

For each of the models considered, conditional movement of the prey was based on relative resource abundance. It was found that only in the absence of conditional movement of the prey did the systems reach an IFD. In nature it cannot be expected that prey species will not move, so my conditional movement strategies are not maximally adaptive for these systems. Instead random discrete diffusion in complement with conditional movement of the prey species could be considered. Adding random discrete diffusion may lead to more realistic results, however I believe that the general findings discussed in this thesis would still hold true. Further, the question of which movement strategy is best used to represent prey and predator species has been, and is currently, a topic of discussion by other researchers in this field [2, 10, 16], but is not the focus of this thesis.

The focus of this thesis is on the "leapfrogging" distribution of the predators. As in previous research [3, 11, 12, 14, 15, 24], when the single-chain system is in IFD the predators exhibit the strongest "leapfrogging" ($C = 1$) and outside of IFD predators over-match or under-match the resource. As conditional prey movement was increased ($d > 0$) C increased from 1 which implies that the predators over-aggregated in the best quality patch compared to IFD. Since the prey's movement here was based on the resource, as the prey become more sensitive to movement information (i.e d is increased) more prey move to the patch with greater abundance of resource. This in turn increases the birth rate of the prey in that patch and in order to offset this increased birth rate the predator's birth rates in that patch must also increase causing the spatial distribution to fall away from IFD and over-aggregate in the best quality patch. While the prey movement rate (d) had a large effect on the predators "leapfrogging" distribution, the predator movement rate (D) had no effect on C . Regardless of the value of D the predators stop moving if the prey's distribution becomes

uniform across the two patches, so the value of D does not affect the equilibrium distribution of the predators if the prey are uniformly distributed. However, the predators fall away from an IFD when $d > 0$ because the prey reach a uniform distribution between patches with abundances below their IFD, which does not allow the predators to reach their IFD, and so changes the degree to which they are “leapfrogging” ($C = 1$ only when an IFD is reached). In the cases with no conditional movement both the predators and the prey can reach IFD.

The two-chain model made predictions that were very similar to those of the single-chain model when a steady state equilibrium was reached; in the two-chain model, the predators, both individually and in aggregate, were predicted to undergo the leapfrog effect, and were observed to undergo perfect resource matching when the prey were not moving. Again when the prey were allowed to move ($d > 0$), the system either reached an equilibrium that was not an IFD or did not reach an equilibrium at all. The movement sensitivity of the predators (D) again did not have an effect on C for similar reasons to those discussed above. This implies that both the predator species in aggregate and independently act the same way in the two-chain model as in the single-chain model. Given that the two-chain and single-chain models act similarly, it can be said that the “leapfrogging” phenomenon found in the single-chain model can be translated to the predators individually, and in aggregate, in the two-chain model.

In the web model, simply making one predator species more adept at consuming and/or reproducing would lead to the extinction of one of the prey species and/or one of the predator species. Intuitively, since one of the prey and predator species are more adept they will be the ones to survive. Instead, I considered two predator species whose distinction was in the prey that they “preferred”. While both predator species consume both of the prey species (since they are generalists to a certain degree) each predator has higher rates of consumption and reproduction steaming from one of the prey. This in turn also creates a distinction between the two prey species, since they are consumed at different rates from the two different predator species. In this system each of the species will exist, and I observed the system to exhibit an oscillatory behavior. This oscillatory behavior can be explained by the fact that since the prey and predators do not start with equal abundances the prey

with the higher starting abundance will allow the predator who more strongly consumes that prey to do better until there are too many of those predators which causes the oscillations. In the very specific case where equilibrium abundances are equal to begin, I will have a steady state equilibrium where movement does not matter since all abundances are equal, and so is a trivial case. Since the predators individually exhibit periodic oscillations and the resource abundance is constant, the predator species individually cannot exhibit leapfrogging. Instead I focused on the predator spatial distribution in aggregate, which was found to exhibit leapfrogging, regardless of the movement rates of the predators, and in the absence of prey movement. The movement rates, D , fail to affect the leapfrogging phenomenon since, similarly to the past two systems, the predators are moving based on the sum of the prey and the prey in aggregate are uniformly distributed between the two patches. Again similarly to the previous two systems, as the prey movement rate is increased the system falls away from IFD and so falls away from leapfrogging but still undergoes resource matching to a degree.

Previous research has discovered that in single-chain models predators exhibiting IFD will also exhibit the “leapfrogging” phenomenon. Here, I have ascertained that “leapfrogging” will also be the IFD distribution of predators in more complex systems. Further, predators in aggregate will always exhibit some degree of resource matching, while predators individually may fail to exhibit resource matching in highly complex systems like the web model where no steady state equilibrium can be reached. In general my research has found that if we are dealing with the spatial distribution of individual predator species in systems more complicated than the two-chain system *should not* always be modeled with the simpler single-chain system. Yet if we are simply dealing with the spatial distribution of predators in aggregate, then they *can* be modeled with the simpler single-chain system.

5 Conclusions

Previous research [3, 11, 12, 14, 15, 18, 24] has looked at single-chain systems and answered questions about IFDs and the behaviors of predators in such systems. It was found that when the predator species reaches its IFD it will be more closely matching the distribution

of the resource (which the prey consume), which is known as “leapfrogging”. I have sought to take the results around this idea of “leapfrogging” and understand if the single-chain system is a good approximation of more complicated systems that are much more likely to occur in nature. The research discussed in this thesis shows us that the single-chain system *should not* be used to model the predators individually in more complicated systems, though single-chain systems *can* be used to model predators in aggregate for more complicated systems that are expected to reach IFD. Through the research discussed in this thesis we can see that the results found in previous research must be looked at in the very specific case of a single-chain system, or for aggregate predators in systems that are expected to reach IFD.

The findings discussed in this thesis were found with the mathematical assumption that both prey and predator species from one patch to the next will have the same consumption and death parameter. Biologically, this means that both prey and predator species are the same from one patch to the next, which is a reasonable assumption especially since our patches are close enough to allow for movement. The research discussed in this thesis has also led to some more interesting questions that include: What changes in the models when the species in one patch are allowed to have different parameters than the species in the other patch? When do systems with conditional movement reach an equilibrium and when do they fail to reach an equilibrium? What makes these systems fail or succeed to reach an equilibrium? These questions will be the focus of future work.

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