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The Effects of Harvesting on Ecological Communities

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THE EFFECTS OF HARVESTING ON ECOLOGICAL COMMUNITIES

By

Douglas Robert Scheib

A DISSERTATION

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of the University of Miami
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Doctor of Philosophy

THE EFFECTS OF HARVESTING ON ECOLOGICAL COMMUNITIES

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In this paper, we derive and study a model for three species interacting via intraguild predation. We assume logistic growth for both the resource and consumer species, and functional responses with saturation, interspecific interference, and intraspecific interference for the predator-prey interactions. This leads to Beddington-DeAngelis-type functional responses. We consider local and global properties of the resource-consumer subsystem, and give conditions for permanence. We then consider permanence in the full system, along with the effects varying some of the parameters has on the invasibility and exclusion of each species. We also look at the effects that harvesting each species in the system has on the ecological community. We then consider a linear food chain, apparent competition, resource competition, and interspecific killing as special cases of our intraguild predation model. Finally, we discuss the biological mechanisms underlying our results.

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Chapter 1

Introduction and Background

1.1 Introduction

The mathematical study of population dynamics dates back over 200 years. The work of Malthus in the late 1790s focused on modeling human populations and in the 1830s and 1840s, Verhulst used the logistic equation to study self-regulating populations. As mathematical theory has grown and the tools needed to study evermore complex species interactions has developed, theoretical models have also evolved. In the early part of the 20th century, Lotka and Volterra proposed a model for an interacting predator and prey species, using a system of coupled ordinary differential equations. Since then, many more models have been proposed and studied representing various types of species interactions. One type of species interaction known to be ubiquitous in nature is intraguild predation. In [56], Rosenheim defines intraguild predation as being a species interaction which occurs when two predators that compete for a shared resource also engage in predator-prey interactions with each other. The intraguild competitor at the higher trophic level is commonly referred to as the IGpredator while the other intraguild competitor is the IGprey. We will use the terminology predator to refer to the IGpredator and consumer to refer to the IGprey.

Many examples of intraguild predation are known to exist in ecological communities involving mammals, fish, insects, and plants, among other species. Among the many examples are the following. In the northern prairies of the United States and Canada, coyotes (*Canis latrans*) and bobcats (*Lynx refus*) compete with racoons (*Procyon lotor*) for small mice, juvenile birds, eggs, frogs, crayfish and crabs. But coyotes and bobcats also feed upon racoons, who are an invasive species [24, 39, 42]. In Guam, brown tree snakes (*Boiga irregularis*) compete with mangrove monitor lizards (*Varanus indicus*) for small vertebrates, invertebrates, and bird and reptile eggs. But, both species consume each other in a form of intraguild predation known as mutual intraguild predation [23]. In Australia, China, Cyprus, Italy, Morocco, New Zealand, Spain, and South Africa, Eurasian perch (*Perca fluvitilis*) is an invasive species who competes with freshwater fish such as common bully (*Gobiomorphis cotidianus*) for zooplankton and macroinvertebrates. But eurasian perch also consume freshwater fish [40]. Many more examples are given by Bampfylde and Lewis in [7] and Polis, Holt, and Myers in [54].

In this paper, we will study a model for three species interacting via intraguild predation. We will being by deriving the model using a time budget analysis similar to the ones used by Holling [32] and Beddington [8]. We will assume saturation effects for the consumers and predators interacting with the resource, as well as with each other. We will also assume the consumers and predators exhibit interference competition among themselves. This will lead to Beddington-DeAngelis-type nonlinear functional responses. Much work has been done to understand how the Beddington-DeAngelis functional response affects the dynamics of interacting species. The seminal work by Cantrell and Cosner [14] established conditions under which a predator-prey system with logistic growth for the prey species and Beddington-DeAngelis function response will be permanent. They discussed how intraspecific interference affects the local stability of the interior equilibrium, how it affects global asymptotical stability of the

interior equilibrium, and proved the existence of at least one periodic orbit. Since then, Hwang [37] has proven the uniqueness of the periodic orbit and other models have confirmed that mutual interference can stabilize predator-prey interactions and can lead to Turing spatial patterns [3, 20]. Additionally, models with Beddington-DeAngelis functional response can exhibit complex dynamics, including Saddle-node, Transcritical, HopfAndronov, and BogdanovTakens bifurcations and chaos [29, 44, 50, 69].

One of the earliest mathematical treatments of intraguild predation was by Holt and Polis in [35] who found that intraguild predation could destabilize a positive equilibrium in a Lotka-Volterra model with linear functional responses. They conjectured that nonlinear functional responses could lead to more robust coexistence of all three species than they found in their paper. In [47], McCann and Hastings incorporated nonlinear functional responses and showed that omnivory could in fact work as a stabilizing agent. Other studies of intraguild predation, such as [2, 6, 7, 34, 41], have also incorporated nonlinear functional responses. These studies have also confirmed the suspicions of Holt and Polis, although the functional responses used in those studies turn out to be special cases of the functional responses we use in this paper.

We will also follow Holt and Polis' suggestion of incorporating an alternative food source exclusively for the consumer species. The addition of alternative food sources has been studied in [18, 30, 34]. In these studies, the alternative food sources were incorporated into the models via additional dynamic equations. These studies found that having an alternative food source for the consumer species can lead to coexistence even when the consumer species is not superior to the predator in exploitation competition. In this paper, we will take a different approach. We will assume that in the absence of the basal resource or the top predator, the consumer species grows logistically. Thus, we will have both the resource and consumer species growing logistically in the absence of each other and the predator. This modeling assumption seems

to be rare. Magal, Ruan, and Cosner [45] make such an assumption, although they do so in the context of a two-species predator-prey model. Bampfylde and Lewis [7] use logistic growth for the consumer and predator species in an intraguild predation model, although they do not model the resource explicitly.

In studying our intraguild predation model, we will use topics and techniques from Differential Equations and Dynamical Systems. Among these will be standard topics such as equilibria and stability, bifurcations, linearization, Lyapunov functions, and sub- and supersolutions. For more information, see [28, 53, 66]. Because of the complexity of the model under consideration, it will also be necessary to establish coexistence from the perspective of permanence. In the following section, we give some necessary background on permanence. The discussion on permanence will follow from [12, 13, 15, 36, 59].

Aside from the ecological reasons for studying intraguild predation, or any model of interacting species for that matter, there can also be practical reasons. There are many people who harvest members of ecological communities for food, business, sport, population control, or other reasons. Among these species that are harvested by humans are members of ecological communities exhibiting intraguild predation. It is important to understand the effects of harvesting on ecological communities before such actions are undertaken as harvesting species at one level can have unintended consequences at another level. In [52], Palomares et. al. study an intraguild predation ecosystem where Iberian lynx (*Felis pardina*) and Egyptian mongooses (*Herpestes ichneumon*) compete for European rabbits (*Oryctolagus cuniculus*) in southwestern Spain. Iberian lynx also consume Egyptian mongooses [51]. Rabbits are of economic concern because they are game for many hunting areas and are the primary food source for many endangered predators [19]. Palomares et. al. found that when the lynx is not present, the rabbits suffered greater mortality from predation and lower growth rate. Thus, if preservation of rabbits is of economic interest then harvesting

the lynx may not be a good strategy, despite one's initial instinct that reducing one of the rabbits' predators should benefit the rabbits.

Another ecological community with intraguild predation in which harvesting takes place consists of the European green crab (*Carcinus maenas*) as the predator species, the Shore crab (*Hemigrapsus sanguineus, H. oregonensis*) as the consumer species, and the resource is any combination of mussels, clams, scallops, snails, isopods, barnacles, or algae [26, 27, 38]. According to [25, 33, 43], European green crabs are known to have negative effects on clams, both soft-shelled and hard-shelled, scallops, and other commercially harvested species. More specifically, green crabs consume, among other species, blue mussel (*Mytilus edulis*), soft-shell clam (*Mya arenaria*), and manila clam (*Venerupis philippinarum*) [43, 48]. In 1996, crab predation in Tomales Bay resulted in a nearly 40% loss in annual production of manila clams for one producer, and it is estimated that the average annual losses to shellfisheries on the East Coast due to green crab predation are $22.6 million [43]. In this scenario, it is of interest to understand the effects of harvesting at two levels of the community: harvesting the resource for commercial reasons and harvesting the predators to control their biological invasion. More examples of harvesting or species removal within communities exhibiting intraguild predation can be found in [1, 16, 55, 67].

In our model, we will consider constant-effort harvesting, as opposed to constant-yield harvesting, which is also known as constant-quota harvesting. This is done for two reasons. One is analytical tractability. Some early mathematical work on constant-yield harvesting was done by Brauer and Soudack [11, 10] in 1979. Because they were working with fairly nice 2-D predator-prey systems, they were able to treat many of the cases which can arise under constant-yield prey harvesting or constant-yield predator harvesting. But even simple 2-D models with constant-yield harvesting can exhibit complicated dynamics, such as Bogdanov-Takens bifurcations [68]. In our case, the system yields prohibitively complicated calculations, even in the case

without harvesting. With constant-yield harvesting, obtaining useful information becomes even more difficult and prohibitive. The second reason is to preserve the extinction equilibrium at the origin in a natural way. It is clear that biologically, the origin is always an equilibrium point and with constant-effort harvesting, it remains so mathematically.

Constant effort harvesting has been used in many populations models with harvesting. Some of the earliest work was done by Schaefer in [58], who studied a single-species model with a population growing logistically and subject to constant-effort harvesting. May et. al. [46] followed this work with a number of multi-species models incorporating constant-effort harvesting. Often, models of interacting species which incorporate constant-effort harvesting are interested in obtaining information about the maximum sustainable yield (MSY) for the harvested population. Though interesting, MSY is beyond the scope of our current analysis. For more information about MSY and other economically interesting questions related to harvesting, the reader is referred to the book by Clark [17].

In addition to studying ecological communities exhibiting intraguild predation, we will also study models for a linear food chain (where the predator species does not consume the resource), resource competition (where the predators do not feed upon the consumer species), and apparent competition (where consumers do not eat the resource). By setting certain attack rates in the model to zero, we will be able to study these types of ecological communities as special cases of intraguild predation. Just as intraguild predation models can exhibit chaos [64], these "simpler" ecological communities can exhibit dynamics can also be quite complicated. For instance, the work of Hastings and Powell [31] found chaos in a three-species food chain, and Takeuchi and Adachi [63] found periodic motion and chaos in a model for apparent competition. Many models have studied the effects of harvesting on ecological communities which are special cases of intraguild predation, including

Another ecological interaction which can be studied as a special case in our model is interspecific killing. Intraguild predation where the predator kills but does not consume the consumer species has been previously documented. For example, Eurasian lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) compete for roe deer (*Capreolus capreolus*) and mountain hares (*Lepus timidus*), but the lynx are also known to kill without consuming the fox [62]. Another example occurs between arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*), which compete for food [21, 22, 65, 60], but where red foxes are known to attack without consuming arctic foxes. To study these cases, the conversion rate from consumer to predator species will be small or zero.

1.2 Background on Permanence

Since our model will consist of a system of ordinary differential equations, we will cast our discussion of permanence in the light of flows and dynamical systems. The discussion could equally well be applied to semiflows and semi-dynamical systems if our system consisted of partial differential equations instead.

Let Y be a complete metric space and suppose we can write Y as $Y = Y_0 \cup \partial Y_0$, where Y_0 is open. Let $\pi : Y \times \mathbb{R} \to Y$ be a flow under which Y_0 and ∂Y_0 are forward invariant.

Definition 1.1. *Let (Y, d) be a metric space and let π be a dynamical system on (Y, d). A set $\mathcal{A}$ which is compact, invariant under π and such that for all bounded subsets U of Y,*

$$\lim_{t \to \infty} \sup_{u \in U} \inf_{v \in \mathcal{A}} d\left(\pi(u, t), v\right) = 0$$

is called a global attractor for π.

Definition 1.2. *We say that π is dissipative if there is a bounded subset U of Y so that for any $u \in Y$, $\pi(u, t) \in U$ for all sufficiently large t.*

Theorem 1.1 (Bilotti and La Salle, 1971)**.** *If Y is a complete metric space, π is dissipative, and for all $t > t_0 \geq 0$, the set $\pi(U, t) = \{\pi(u, t) \ : \ u \in U\}$ is precompact if U is bounded, then π has a nonempty global attractor.*

Definition 1.3. *A dynamical system π is called weakly persistent if $\forall \ y \ \in \ Y$, $\limsup\limits_{t \to \infty} d\left(\pi(y, t), \partial Y_0\right) > 0$. We say that π is persistent if $\limsup$ is replaced by $\liminf$ in the definition of weak persistence. We call π uniformly persistent if $\forall \ y \in Y$, $\exists \ \epsilon > 0$ such that $\liminf\limits_{t \to \infty} d\left(\pi(y, t), \partial Y_0\right) > \epsilon$.*

Definition 1.4. *We say that π is permanent if it is uniformly persistent and dissipative.*

Before we can state the theorem which we will be using to establish permanence, we need the following definitions.

Definition 1.5. *A collection $\mathcal{U}$ of subsets of a space Y is said to be a covering of Y if the union of the elements of $\mathcal{U}$ is equal to Y.*

Let $\mathcal{U} = \{\mathcal{U}_k\}_{k=1}^{n}$ where $\mathcal{U}_k \subset Y$. We call $\mathcal{U}$ a covering of Y if $Y = \cup_{k=1}^{n} \mathcal{U}_k$.

Definition 1.6. *Suppose an invariant set M for π has a neighborhood U such that M is the maximal invariant subset of U. The M is said to be isolated.*

Notation: $\omega\left(\partial Y_0\right) = \cup_{u \in \partial Y_0} \omega(u) \subseteq \partial Y_0$

Definition 1.7. *Suppose the sets M_k $(k = 1, .., N)$ are pairwise disjoint and are isolated and invariant with respect to π on ∂Y_0 and Y. If $\omega\left(\partial Y_0\right)$ has a covering $M = \cup_{k=1}^{N} M_k$ then $\omega\left(\partial Y_0\right)$ is called isolated and M is called an isolated covering.*

Definition 1.8. *If N_1 and N_2 are two, not necessarily distinct, isolated invariant sets then the set N_1 is said to be chained to N_2 if $\exists \ u \notin N_1 \cup N_2$ with $u \in W^u(N_1) \cap W^s(N_2)$.*

Notation: If N_1 is chained to N_2 then we write $N_1 \to N_2$.

Definition 1.9. *A finite sequence $N_1, \ldots, N_k$ of isolated invariant sets is a chain if $N_1 \to N_2 \cdots \to N_k$. The chain is a cycle if $N_k = N_1$.*

Definition 1.10. *The set $\omega(\partial Y_0)$ is said to be acyclic if there exists an isolated covering $\cup_{k=1}^{N} M_k$ such that no subset of $\{M_k\}$ is a cycle.*

We are now ready to state the following theorem due to Butler, Freedman, and Waltman [12].

Theorem 1.2. *Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ where Y_0 is open. Suppose that a flow on Y leaves both Y_0 and ∂Y_0 forward invariant, maps bounded sets in Y to precompact sets for $t > 0$, and is dissipative. If in addition*

  (i) $\omega(\partial Y_0)$ *is isolated and acyclic,*

  (ii) $W^S(M_k) \cap Y_0 = \emptyset$ *for all k, where $\cup_{k=1}^{N} M_k$ is the isolated covering used in the definition of acyclicity of ∂Y_0,*

then the flow is permanent; i.e., there exists $\epsilon > 0$ such that any trajectory with initial data in Y_0 will be bounded away from ∂Y_0 by a distance greater than ϵ for t sufficiently large.

<u>Note</u>: At the boundary equilibria, at least one of the species is absent. Condition (ii) in Theorem (1.2) says that near each boundary equilibrium, each species which is absent at that equilibrium must be able to invade the system. So condition (ii) is a condition about invasibility. Essentially what we need is for the boundary to be repelling and to ensure that we do not have any heteroclinic orbits in the boundary.

In studying the 2-dimensional resource - consumer subsystem, we will take $Y_0 = \mathbb{R}_+^2$ so that $\partial Y_0 = \{(R,0) : R \geq 0\} \cup \{(0,C) : C \geq 0\}$. We will see that $\omega(\partial Y_0)$ will consist of the non-dimensionalized equilibria $(0,0)$, $(1,0)$, and $(0,1)$. Clearly, $\omega(\partial Y_0)$ is isolated. We will see that for all $(R,0) \in \{(R,0) : 0 < R < 1\}$, $\frac{dR}{dt} > 0$ and for all $(R,0) \in \{(R,0) : R > 1\}$, $\frac{dR}{dt} < 0$. Thus, any trajectory in $\{(R,0) : R \geq 0\}$ other

than $(0,0)$ approaches $(1,0)$. For all $(0,C) \in \{(0,C) : 0 < C < 1\}$, $\frac{dC}{dt} > 0$ and for all $(0,C) \in \{(0,C) : C > 1\}$, $\frac{dC}{dt} < 0$. Thus, any trajectory in $\{(0,C) : C \geq 0\}$ other than $(0,0)$ approaches $(0,1)$. It follows from these features of that ∂Y_0 is acyclic.

In studying the full 3-dimensional model, we will take $Y_0 = \mathbb{R}^3_+$ so that $\partial Y_0 = \{(R,C,0) : R \geq 0, \ C \geq 0\} \cup \{(0,C,P) : C \geq 0, \ P \geq 0\} \cup \{(R,0,P) : R \geq 0, \ P \geq 0\}$. We shall return to acyclicity in this case, which requires a bit more work than it did in the 2-dimensional case, in chapter 4.

Chapter 2

The Model

2.1 Construction of the Model

The model we will be interested in studying is a three-species model for intraguild predation. We will assume that the basal resource grows logistically in the absence of any predators. We will also assume that the consumer species is a generalist who grows logistically in the absence of basal resource or predation, but who also exploits the basal resource as part of its diet. The top predator is a specialist, feeding on both the basal resource and the consumer species, who has a mortality rate proportional to its population density. All three model species will also be subjected to constant effort harvesting. We let R represent the density of the basal resource, C represent the density of the consumer species, and P represent the density of the top predator. Table 2.1 gives a description of the parameters which will be used in the general form of our model system which we will be interested in studying. That model system is

Table 2.1: Description of parameters in system (2.1)

Parameter	Description
r_R	intrinsic growth rate of basal resource in the absence of predation
r_K	intrinsic growth rate of consumer species in the absence of basal resource and predation
K_R	environmental carrying capacity for basal resource
K_C	environmental carrying capacity for consumer species
$f_{RC}(R,C,P)$	functional response of consumer species to basal resource
$f_{RP}(R,C,P)$	functional response of top predator to basal resource
$f_{CP}(R,C,P)$	functional response of top predator to consumer species
α_{RC}	conversion efficiency of basal resource to consumer species
α_{RP}	conversion efficiency of basal resource to top predator
α_{CP}	conversion efficiency of consumer species to top predator
m_P	mortality rate of top predator
H_R	rate at which the basal resource is harvested
H_C	rate at which consumers are harvested
H_P	rate at which predators are harvested

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - f_{RC}(R,C,P) - f_{RP}(R,C,P) - H_R R$$

$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) + \alpha_{RC} f_{RC}(R,C,P) - f_{CP}(R,C,P) - H_C C \qquad (2.1)$$

$$\frac{dP}{dt} = \alpha_{RP} f_{RP}(R,C,P) + \alpha_{CP} f_{CP}(R,C,P) - m_P P - H_P P$$

2.2   Derivation of the Functional Responses

In order to derive the functional response of the consumer species to the basal resource, the top predator to the basal resource, and the top predator to the consumer, we use a time budget analysis similar to the ones used by Holling [32] and Beddington [8]. A summary of parameters can be found in Table (2.2).

2.2.1 Consumer-Resource Functional Response

The total time consumers spend attempting to forage for food, T_C, consists of four components: the time they spend searching for the basal resource, t_{RCS}, the time they spend handling the basal resource, t_{RCH}, the time they spend interacting with other consumers, t_C, and the time they spend avoiding predation, t_{PC}. Thus, we have that

$$T_C = t_{RCS} + t_{RCH} + t_C + t_{PC} \tag{2.2}$$

The number of basal resource encountered by consumers during time T_C, N_{RC}, depends on the rate at which consumers attack basal resource, e_{RC}, the part of T_C consumers spend searching for basal resource, and the density of the basal resource. The number of other consumers encountered by consumers during time T_C, N_C, depends on the rate at which consumers encounter other consumers, e_C, the part of T_C consumers spend interacting with other consumes, and the density of the consumer population. The number of predators encountered by consumers during time T_C, N_{PC}, depends on the rate at which consumers encounter predators, e_{CP}, the time consumers spend avoiding or escaping from predators, and the density of the predator population. Thus, we have the following relations.

$$N_{RC} = e_{RC} t_{RCS} R$$

$$N_C = e_C t_{RCS} C$$

$$N_{PC} = e_{CP} t_{RCS} P$$

The part of T_C consumers spend handling encountered basal resource depends on the number of encounters between consumers and basal resource during T_C and the length of time required for consumers to handle each encountered basal resource, h_{RC}. The part of T_C consumers spend interacting with other consumers depends on the number of other consumers encountered by consumers during T_C and the length

of time for each interaction between consumers, h_C. The part of T_C consumers spend avoiding predation depends on the number of predators encountered by consumers during T_C and the length of time required for consumers to avoid or escape each encountered predator, h_{PC}. This gives us

$$t_{RCH} = N_{RC}h_{RC} = e_{RC}h_{RC}t_{RCS}R \tag{2.3}$$

$$t_C = N_Ch_C = e_Ch_Ct_{RCS}C \tag{2.4}$$

$$t_{PC} = N_{PC}h_{PC} = e_{CP}h_{PC}t_{RCS}P \tag{2.5}$$

Thus, substituting equations (2.3), (2.4), and (2.5) into equation (2.2), we get

$$T_C = t_{RCS} + e_{RC}h_{RC}t_{RCS}R + e_Ch_Ct_{RCS}C + e_{CP}h_{PC}t_{RCS}P$$
$$= t_{RCS}\left(1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P\right)$$

The per capita rate of encounters of consumers with basal resource is the number of basal resource encountered by consumers during time T_C, N_{RC}, divided by the time T_C. Thus the consumer functional response to the basal resource is

$$\frac{N_{RC}}{T_C} = \frac{e_{RC}t_{RCS}R}{t_{RCS}\left(1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P\right)}$$
$$= \frac{e_{RC}R}{1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P}$$

Thus, the overall rate at which consumers encounter the basal resource is

$$f_{RC}(R,C,P) = \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P} \tag{2.6}$$

2.2.2 Predator-Resource Functional Response

The total time predators spend attempting to forage for food, T_P, consists of four components: the time they spend searching for food (basal resources or consumers), t_{PS}, the time they spend handling encountered basal resource, t_{RPH}, the time they spend handling encountered consumers, t_{CPH}, and the time they spend interacting with other predators, t_P. Thus, we have that

$$T_P = t_{PS} + t_{RPH} + t_{CPH} + t_P \tag{2.7}$$

The number of encounters with the basal resource by predators during time T_P depends on the rate at which predators attack basal resource, e_{RP}, the part of T_P consumers spend searching for basal resource, and the density of the basal resource. The number of consumers encountered by predators during time T_P depends on the rate at which predators attack consumers, e_{CP}, the part of T_P predators spend searching for consumers, and the density of the consumer population. The number of other predators encountered by predators during time T_P depends on the rate at which predators encounter other predators, e_P, the time predators spend interacting with other predators, and the density of the predator population. Thus, we have the following relations.

$$N_{RP} = e_{RP}t_{PS}R$$
$$N_{CP} = e_{CP}t_{PS}C$$
$$N_P = e_P t_{PS}P$$

The part of T_P predators spend handling encountered basal resource depends on the number of encounters between predators and basal resource during T_P and the length of time required for predators to handle each encountered basal resource,

h_{RP}. The part of T_P predators spend handling encountered consumers depends on the number of consumers encountered by predators during T_P and the length of time required for predators to handle each encountered consumer, h_{CP}. The part of T_P predators spend interacting with other predators depends on the number of other predators encountered by predators during T_P and the length of time for each interaction between predators, h_P. This gives us

$$t_{RPH} = N_{RP}h_{RP} = e_{RP}h_{RP}t_{PS}R \tag{2.8}$$

$$t_{CP} = N_{CP}h_{CP} = e_{CP}h_{CP}t_{PS}C \tag{2.9}$$

$$t_P = N_P h_P = e_P h_P t_{PS}P \tag{2.10}$$

Thus, substituting equations (2.8), (2.9), and (2.10) into equation (2.7), we get

$$T_P = t_{PS} + e_{RP}h_{RP}t_{PS}R + e_{CP}h_{CP}t_{PS}C + e_P h_P t_{PS}P$$
$$= t_{PS}\left(1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P\right)$$

The per capita rate of encounters of predators with basal resource is the number of basal resource encountered by predators during time T_P, N_{RP}, divided by the time T_P. Thus the predator functional response to the basal resource is

$$\frac{N_{RP}}{T_P} = \frac{e_{RP}t_{PS}R}{t_{PS}\left(1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P\right)}$$
$$= \frac{e_{RP}R}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P}$$

Thus, the overall rate at which the basal resource is encountered by predators is

$$f_{RP}(R, C, P) = \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} \tag{2.11}$$

2.2.3 Predator-Consumer Functional Response

The per capita rate of encounters of predators with consumers depends on the preda-
tor's time utilization, which remains the same as in the previous section. In this case,
the predator functional response to the consumers is

$$\frac{N_{CP}}{T_P} = \frac{e_{CP}t_{PS}C}{t_{PS}\left(1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP\right)}$$
$$= \frac{e_{CP}C}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP} \qquad (2.12)$$

Thus, the overall rate at which predators encounter consumers is

$$f_{CP}(R,C,P) = \frac{e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP} \qquad (2.13)$$

2.3 The Model and Special Cases

Upon substituting equations (2.6), (2.11), and (2.13) into system (2.1) gives us the
model system which we will focus our attention on.

$$\frac{dR}{dt} = r_RR\left(1 - \frac{R}{K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P}$$
$$\quad - \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP} - H_RR$$
$$\frac{dC}{dt} = r_CC\left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_Ch_CC + e_{CP}h_{PC}P} \qquad (2.14)$$
$$\quad - \frac{e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP} - H_CC$$
$$\frac{dP}{dt} = \frac{\alpha_{RP}e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP} + \frac{\alpha_{CP}e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_Ph_PP}$$
$$\quad - m_PP - H_PP$$

In the case where the top predator does not feed on the basal resource; i.e., when
$e_{RP} = 0$, then the top predator feeds upon only the consumer and the consumers

Table 2.2: Summary of parameters used in the derivation of the functional responses.

Parameter	Description
T_C	time consumers spend searching for resources, handling captured resources, interacting with other consumers, and avoiding predation
T_P	time predators spend searching for resources, handling captured resources, searching for consumers, handling captures consumers, and interacting with other predators
t_{RCS}	the part of T_C consumers spend searching for basal resource
t_{RCH}	the part of T_C consumers spend handling encountered basal resource
t_C	the part of T_C consumers spend interacting with other consumers
t_{PC}	the part of T_C consumers spend avoiding predation
t_{PS}	the part of T_P predators spend searching for food (basal resource or consumers)
t_{RPH}	the part of T_P predators spend handling encountered basal resource
t_{CPH}	the part of T_P predators spend handling encountered consumers
t_P	the part of T_P predators spend interacting with other predators
e_{RC}	rate at which consumers attack basal resource
e_C	rate at which consumers encounter other consumers
e_{CP}	rate at which consumers encounter predators or predators attack consumers
e_{RP}	rate at which predators attack basal resource
e_P	rate at which predators encounter other predators
N_{RC}	number of basal resource encountered by consumers during T_C
N_C	number of other consumers encountered by consumers during T_C
N_{PC}	number of predators encountered by consumers during T_C
N_{RP}	number of basal resource encountered by predators during T_P
N_{CP}	number of consumers encountered by predators during T_P
N_P	number of other predators encountered by predators during T_P
h_{RC}	length of time for consumers to handle each encountered basal resource
h_C	length of time required for each interaction between consumers
h_{PC}	length of time required for consumers to avoid/escape each encountered predator
h_{RP}	length of time required for predators to handle each encountered basal resource
h_{CP}	length of time required for predators to handle each encountered consumer
h_P	length of time required for each interaction between predators

feed upon only the basal resource. In such a case, there is no competition between the consumers and top predators. This represents a linear food chain and the model system becomes

$$
\begin{aligned}
\frac{dR}{dt} &= r_R R \left(1 - \frac{R}{K_R} \right) - \frac{e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P} - H_R R \\
\frac{dC}{dt} &= r_C C \left(1 - \frac{C}{K_C} \right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P} \\
&\quad - \frac{e_{CP} CP}{1 + e_{CP} h_{CP} C + e_P h_P P} - H_C C \\
\frac{dP}{dt} &= \frac{\alpha_{CP} e_{CP} CP}{1 + e_{CP} h_{CP} C + e_P h_P P} - m_P P - H_P P
\end{aligned}
\tag{2.15}
$$

In the case where the consumers do not feed on the basal resource; i.e., when $e_{RC} = 0$, then the top predator preys upon both the basal resource and the consumers, but the basal resource has no other predators. In such a case, the basal resource and the consumers compete for refuges and for survival from the top predator. This represents apparent competition and the model system becomes

$$
\begin{aligned}
\frac{dR}{dt} &= r_R R \left(1 - \frac{R}{K_R} \right) - \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} - H_R R \\
\frac{dC}{dt} &= r_C C \left(1 - \frac{C}{K_C} \right) - \frac{e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} - H_C C \\
\frac{dP}{dt} &= \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} + \frac{\alpha_{CP} e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} \\
&\quad - m_P P - H_P P
\end{aligned}
\tag{2.16}
$$

In the case where the top predator does not feed on the consumers; i.e., when $e_{CP} = 0$, then the consumers have no predators and the only food source for the predators is the basal resource. In such a case, the consumers and predators compete for the basal resource. This represents resource competition and the model becomes

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C}$$
$$\quad - \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R + e_P h_P P} - H_R R$$
$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C} - H_C C \qquad (2.17)$$
$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_P h_P P} - m_P P - H_P P$$

In the case where the top predator attacks but does not consume the consumers; i.e., when $\alpha_{CP} = 0$, then the consumers experience predation but the predators do not experience growth from their interactions with the consumers. In such a case, we have interspecific killing and the model becomes

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P}$$
$$\quad - \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} - H_R R$$
$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P} \qquad (2.18)$$
$$\quad - \frac{e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} - H_C C$$
$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} - m_P P - H_P P$$

2.4   Non-dimensionalized Model

To simplify the model, we make the following substitutions for the variables R, C, P, and t:

$$\tilde{R} = \tfrac{1}{K_R} R, \quad \tilde{C} = \tfrac{1}{K_C} C, \quad \tilde{P} = e_P h_P P, \quad \tilde{t} = r_R t$$

From the chain rule we have

$$\frac{d\tilde{R}}{d\tilde{t}} = \frac{d\tilde{R}}{dR} \cdot \frac{dR}{dt} \cdot \frac{dt}{d\tilde{t}} = \left(\frac{1}{K_R}\right)\left(\frac{dR}{dt}\right)\left(\frac{1}{r_R}\right) = \frac{1}{r_R K_R}\frac{dR}{dt}$$

$$\frac{d\tilde{C}}{d\tilde{t}} = \frac{d\tilde{C}}{dC} \cdot \frac{dC}{dt} \cdot \frac{dt}{d\tilde{t}} = \left(\frac{1}{K_C}\right)\left(\frac{dC}{dt}\right)\left(\frac{1}{r_R}\right) = \frac{1}{r_R K_C}\frac{dC}{dt} \quad (2.19)$$

$$\frac{d\tilde{P}}{d\tilde{t}} = \frac{d\tilde{P}}{dP} \cdot \frac{dP}{dt} \cdot \frac{dt}{d\tilde{t}} = (e_P h_P)\left(\frac{dP}{dt}\right)\left(\frac{1}{r_R}\right) = \frac{e_P h_P}{r_R}\frac{dP}{dt}$$

If we plug in the equations in system (2.18) into (2.19) and make the substitutions for the non-dimensionalized parameters, we get

$$\frac{d\tilde{R}}{d\tilde{t}} = \tilde{R}\left(1 - \tilde{R}\right) - \frac{e_{RC}K_C\tilde{R}\tilde{C}}{r_R\left(1 + e_{RC}h_{RC}K_R\tilde{R} + e_C h_C K_C\tilde{C} + \frac{e_{CP}h_{PC}}{e_P h_P}\tilde{P}\right)}$$

$$- \frac{e_{RP}\tilde{R}\tilde{P}}{r_R e_P h_P\left(1 + e_{RP}h_{RP}K_R\tilde{R} + e_{CP}h_{CP}K_C\tilde{C} + \tilde{P}\right)} - \frac{H_R\tilde{R}}{r_R}$$

$$\frac{d\tilde{C}}{d\tilde{t}} = \frac{r_C}{r_R}\tilde{C}\left(1 - \tilde{C}\right) + \frac{\alpha_{RC}e_{RC}K_R\tilde{R}\tilde{C}}{r_R\left(1 + e_{RC}h_{RC}K_R\tilde{R} + e_C h_C K_C\tilde{C} + \frac{e_{CP}h_{PC}}{e_P h_P}\tilde{P}\right)}$$

$$- \frac{e_{CP}\tilde{C}\tilde{P}}{r_R e_P h_P\left(1 + e_{RP}h_{RP}K_R\tilde{R} + e_{CP}h_{CP}K_C\tilde{C} + \tilde{P}\right)} - \frac{H_C\tilde{C}}{r_R}$$

$$\frac{d\tilde{P}}{d\tilde{t}} = \frac{\alpha_{RP}e_{RP}K_R\tilde{R}\tilde{P}}{r_R\left(1 + e_{RP}h_{RP}K_R\tilde{R} + e_{CP}h_{CP}K_C\tilde{C} + \tilde{P}\right)}$$

$$+ \frac{\alpha_{CP}e_{CP}K_C\tilde{C}\tilde{P}}{1 + e_{RP}h_{RP}K_R\tilde{R} + e_{CP}h_{CP}K_C\tilde{C} + \tilde{P}} - \frac{m_P}{r_R}\tilde{P} - \frac{H_P\tilde{P}}{r_R}$$

We now make the following parameter substitutions:

$$\tilde{r} = \frac{r_C}{r_R}, \qquad \tilde{h}_{PCP} = \frac{e_{CP}h_{PC}}{e_P h_P}, \qquad \tilde{h}_{CPP} = \frac{e_{CP}h_{CP}}{e_P h_P}, \qquad \tilde{e}_{RC} = \frac{e_{RC}K_C}{r_R}$$

$$\tilde{e}_{RP} = \frac{e_{RP}}{r_R e_P h_P}, \qquad \tilde{\alpha}_{RC} = \frac{\alpha_{RC}e_{RC}K_R}{r_R}, \qquad \tilde{e}_{PC} = \frac{e_{CP}}{r_R e_P h_P}, \qquad \tilde{\alpha}_{RP} = \frac{\alpha_{RP}e_{RP}K_R}{r_R}$$

$$\tilde{\alpha}_{CP} = \frac{\alpha_{CP}e_{CP}K_C}{r_R}, \qquad \tilde{m}_P = \frac{m_P}{r_R}, \qquad \tilde{h}_{RP} = e_{RP}h_{RP}K_R, \quad \tilde{h}_{RC} = e_{RC}h_{RC}K_R$$

$$\tilde{h}_C = e_C h_C K_C, \quad \tilde{h}_{CP} = e_{CP}h_{CP}K_C, \quad \tilde{h}_{PC} = e_{CP}h_{PC}K_C, \qquad \tilde{H}_R = \frac{H_R}{r_R}$$

$$\tilde{H}_C = \frac{H_C}{r_R}, \qquad\qquad \tilde{H}_P = \frac{H_P}{r_R}$$

This leads to the system

$$\frac{d\tilde{R}}{d\tilde{t}} = \tilde{R}\left(1 - \tilde{R}\right) - \frac{\tilde{e}_{RC}\tilde{C}\tilde{R}}{1 + \tilde{h}_{RC}\tilde{R} + \tilde{h}_{PCP}\tilde{P} + \tilde{h}_C\tilde{C}} - \frac{\tilde{e}_{RP}\tilde{P}\tilde{R}}{1 + \tilde{h}_{RP}\tilde{R} + \tilde{h}_{CP}\tilde{C} + \tilde{P}} - \tilde{H}_R\tilde{R}$$

$$\frac{d\tilde{C}}{d\tilde{t}} = \tilde{r}\tilde{C}\left(1 - \tilde{C}\right) + \frac{\tilde{\alpha}_{RC}\tilde{R}\tilde{C}}{1 + \tilde{h}_{RC}\tilde{R} + \tilde{h}_{CPP}\tilde{P} + \tilde{h}_C\tilde{C}} - \frac{\tilde{e}_{CP}\tilde{P}\tilde{C}}{1 + \tilde{h}_{RP}\tilde{R} + \tilde{h}_{CP}\tilde{C} + \tilde{P}} - \tilde{H}_C\tilde{C}$$

$$\frac{d\tilde{P}}{d\tilde{t}} = \frac{\tilde{\alpha}_{RP}\tilde{R}\tilde{P}}{1 + \tilde{h}_{RP}\tilde{R} + \tilde{h}_{PC}\tilde{C} + \tilde{P}} + \frac{\tilde{\alpha}_{CP}\tilde{C}\tilde{P}}{1 + \tilde{h}_{RP}\tilde{R} + \tilde{h}_{CP}\tilde{C} + \tilde{P}} - \tilde{m}_P\tilde{P} - \tilde{H}_P\tilde{P}$$

For the sake of aesthetics, we drop the tildes while keeping in mind that we are now working with the non-dimensionalized system. This gives us

$$\frac{dR}{dt} = R\left(1 - R\right) - \frac{e_{RC}CR}{1 + h_{RC}R + h_{PCP}P + h_C C} - \frac{e_{RP}PR}{1 + h_{RP}R + h_{CP}C + P} - H_R R$$

$$\frac{dC}{dt} = rC\left(1 - C\right) + \frac{\alpha_{RC}RC}{1 + h_{RC}R + h_{CPP}P + h_C C} - \frac{e_{CP}PC}{1 + h_{RP}R + h_{CP}C + P} - H_C C$$

$$\text{(2.20)}$$

$$\frac{dP}{dt} = \frac{\alpha_{RP}RP}{1 + h_{RP}R + h_{PC}C + P} + \frac{\alpha_{CP}CP}{1 + h_{RP}R + h_{CP}C + P} - m_P P - H_P P$$

Chapter 3

Analysis of 2-D Subsystems

Before studying the dynamics of the full system with harvesting, we study the dynamics of each of the subsystems with one species absent.

3.1   No Basal Resource Subsystem

See Cantrell and Cosner [14] for the following results. (Note: all parameters are in terms of the original, dimensionalized parameters.)

The system we consider here is the following.

$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) - \frac{e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P}$$

$$\frac{dP}{dt} = \frac{\alpha_{CP}e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P} - m_P P \tag{3.1}$$

It is clear from an examination of the isoclines that there will be an equilibrium in the first quadrant, whose C-value is given by

$$C^* = \frac{K_C[r_C e_P h_P \alpha_{CP} + e_{CP}(m_P h_{CP} - \alpha_{CP})]}{2r_C \alpha_{CP} e_P h_P}$$

$$+ \frac{\sqrt{\left(K_C[r_C e_P h_P \alpha_{CP} + e_{CP}(m_P h_{CP} - \alpha_{CP})]\right)^2 + 4K_C m_P r_C \alpha_{CP} e_P h_P}}{2r_C \alpha_{CP} e_P h_P} \tag{3.2}$$

if and only if the isocline for $\frac{dP}{dt} = 0$ becomes positive at some value $C < K_C$, which will be true if and only if

$$\alpha_{CP} e_{CP} K_C > (e_{CP} h_{CP} K_C + 1) m_P. \tag{3.3}$$

Theorem 3.1. *The system (3.1) is always dissipative in the first quadrant. It is permanent if and only if (3.3) holds. If the inequality in (3.3) is reversed then $P \to 0$ as $t \to \infty$.*

Lemma 3.2. *Suppose that (3.3) holds and that*

$$(e_{CP} h_{CP} K_C - 1)(\alpha_{CP} e_{CP} K_C - e_{CP} h_{CP} K_C m_P) - 2 e_{CP} h_{CP} K_C m_P > 0. \tag{3.4}$$

If $e_P h_P$ is sufficiently small then the positive equilibrium of (3.1) is unstable. If in addition $\alpha_{CP} e_{CP} K_C$ is sufficiently large then the equilibrium is an unstable spiral point, and (3.1) has a limit cycle.

Lemma 3.3. *If*

$$e_{CP} h_{CP} K_C \left(1 - C^*\right) < 1 \tag{3.5}$$

then $\left(C^*, P^*\right)$ is globally asymptotically stable.

3.2 No Consumers Subsystem

See Cantrell and Cosner [14] for the following results. (Note: all parameters are in terms of the original, dimensionalized parameters.)

The system we consider here is the following.

$$\begin{aligned}
\frac{dR}{dt} &= r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P} \\
\frac{dP}{dt} &= \frac{\alpha_{RP} e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P} - m_P P
\end{aligned} \tag{3.6}$$

It is clear from an examination of the isoclines that there will be an equilibrium in the first quadrant if and only if the isocline for $\frac{dP}{dt} = 0$ becomes positive at some value $R < K_R$, which will be true if and only if

$$\alpha_{RP} e_{RP} K_R > (e_{RP} h_{RP} K_R + 1) m_P \tag{3.7}$$

Theorem 3.4. *The system (3.6) is always dissipative in the first quadrant. It is permanent if and only if (3.7) holds. If the inequality in (3.7) is reversed then $P \to 0$ as $t \to \infty$.*

Lemma 3.5. *Suppose that (3.7) holds and that*

$$(e_{RP} h_{RP} K_R - 1)(\alpha_{RP} e_{RP} K_R - e_{RP} h_{RP} K_R m_P) - 2 e_{RP} h_{RP} K_R m_P > 0. \tag{3.8}$$

If $e_P h_P$ is sufficiently small then the positive equilibrium of (3.6) is unstable. If in addition $\alpha_{RP} e_{RP} K_R$ is sufficiently large then the equilibrium is an unstable spiral point, and (3.6) has a limit cycle.

Lemma 3.6. *If*

$$e_{RP} h_{RP} K_R \left(1 - R^*\right) < 1 \tag{3.9}$$

then $\left(R^*, P^*\right)$ is globally asymptotically stable.

Note: Here R^* is given by

$$R^* = \frac{K_R[r_R e_P h_P \alpha_{RP} + e_{RP}(m_P h_{RP} - \alpha_{RP})]}{2 r_R \alpha_{RP} e_P h_P}$$
$$+ \frac{\sqrt{\left(K_R[r_R e_P h_P \alpha_{RP} + e_{RP}(m_P h_{RP} - \alpha_{RP})]\right)^2 + 4 K_R m_P r_R \alpha_{RP} e_P h_P}}{2 r_R \alpha_{RP} e_P h_P} \tag{3.10}$$

3.3 No Predators Subsystem

3.3.1 Equilibria

In the case where the predators are absent, the non-dimensionalized system becomes

$$\frac{dR}{dt} = R(1 - R) - \frac{e_{RC}CR}{1 + h_{RC}R + h_C C} \tag{3.11}$$
$$\frac{dC}{dt} = rC(1 - C) + \frac{\alpha_{RC}RC}{1 + h_{RC}R + h_C C}$$

To find the equilibria, we set each of the equations in (3.11) equal to zero and solve the resulting system of simultaneous equations. This gives us equilibria of $(0,0)$, $(1,0)$, $(0,1)$, and $\left(R^*, C^*\right)$, where R^* is a solution of the cubic equation

$$\left(\alpha_{RC}h_C^2 + rh_{RC}^2 e_{RC}\right) R^3$$
$$+ \left(rh_C h_{RC}e_{RC} + 2rh_{RC}e_{RC} - 2\alpha_{RC}h_C^2 - rh_{RC}^2 e_{RC} + 2\alpha_{RC}h_C e_{RC}\right) R^2$$
$$+ \left(rh_C e_{RC} - 2rh_{RC}e_{RC} - rh_C h_{RC}e_{RC} - 2\alpha_{RC}h_C e_{RC} + \alpha_{RC}e_{RC}^2 + \alpha_{RC}h_C^2\right.$$
$$\left. + re_{RC} + rh_{RC}e_{RC}^2\right)R + \left(re_{RC}^2 - re_{RC} - re_{RC}h_C\right) = 0 \tag{3.12}$$

and C^* is given by

$$C^* = -\frac{h_{RC}\left(R^*\right)^2 + (1 - h_{RC})R^* - 1}{h_C R^* + (e_{RC} - h_C)}. \tag{3.13}$$

If we let $h(R) = a_3 R^3 + a_2 R^2 + a_1 R + a_0$, where $a_3 = \alpha_{RC}h_C^2 + rh_{RC}^2 e_{RC}$, $a_2 = rh_C h_{RC}e_{RC} + 2rh_{RC}e_{RC} - 2\alpha_{RC}h_C^2 - rh_{RC}^2 e_{RC} + 2\alpha_{RC}h_C e_{RC}$, $a_1 = rh_C e_{RC} - 2rh_{RC}e_{RC} - rh_C h_{RC}e_{RC} - 2\alpha_{RC}h_C e_{RC} + \alpha_{RC}e_{RC}^2 + \alpha_{RC}h_C^2 + re_{RC} + rh_{RC}e_{RC}^2$, and $a_0 = re_{RC}^2 - re_{RC} - re_{RC}h_C$, then we can rewrite equation (3.12) in the form $h(R) = 0$.

To better understand the equilibria, we plot the resource and consumer nullclines and see under which conditions these graphs intersect. The resource nullclines are

the line $R = 0$ and the curve

$$C = \frac{-h_{RC}R^2 + (h_{RC} - 1)R + 1}{h_C R + (e_{RC} - h_C)}. \tag{3.14}$$

The consumer nullclines are the line $C = 0$ and the curves

$$C = \frac{r(h_{RC}R + 1 - h_C) \pm \sqrt{r^2(h_{RC}R + 1 + h_C)^2 + 4rh_C\alpha_{RC}R}}{-2rh_C}. \tag{3.15}$$

For the moment, we will define $f(R)$ to be the positive branch of the resource nullcline and $g(R)$ to be the positive branch of the consumer nullcline. The positive branch of the consumer nullcline is obtained in the case where the square root in the numerator is subtracted. In order to determine the number of the equilibria from the nullclines we need some properties of these nullclines.

The resource nullcline (3.14) has an R-intercept at $R = 1$, a C-intercept of $C = \frac{1}{e_{RC} - h_C}$, a vertical asymptote at $R = 1 - \frac{e_{RC}}{h_C}$, and a slant asymptote of $C = -\frac{h_{RC}}{h_C}R + \frac{h_{RC}e_{RC} - h_C}{h_C^2}$. It also has a removable discontinuity at the point $\left(-\frac{1}{h_{RC}}, 0\right)$ in the (R, C)-plane. We will abuse the terminology a little here and call the point $\left(-\frac{1}{h_{RC}}, 0\right)$ an R-intercept of the resource isocline.

The consumer nullcline (3.15) has an R-intercept at $R = -\frac{r}{rh_{RC} + \alpha_{RC}}$, C-intercepts at $C = -\frac{1}{h_C}$ and $C = 1$, and a horizontal asymptote of $C = 1 + \frac{\alpha_{RC}}{rh_{RC}}$ as $R \to \infty$.

It is easy to see that the three equilibria we already have, $(0, 0)$, $(1, 0)$, and $(0, 1)$ are recovered from the intersections of the resource nullcline $R = 0$ with the consumer nullcline $C = 0$, the resource nullcline (3.14) with the consumer nullcline $C = 0$ at the resource nullcline's R-intercept $R = 1$, and the resource nullcline $R = 0$ with the consumer nullcline (3.15) at the consumer nullcline's C-intercept $C = 1$, respectively. For any possible interior equilibria, we need to determine if and when the resource nullcline (3.14) intersects the consumer nullcline (3.15). There are several cases to consider in this endeavor.

(1) The resource nullcline's vertical asymptote is less than the resource nullcline's R-intercept of $R = -\frac{1}{h_{RC}}$. This gives the condition that

$$e_{RC} > h_C + \frac{h_C}{h_{RC}}. \tag{3.16}$$

There are two subcases here.

(a) The resource nullcline's C-intercept is greater than the consumer nullcline's C-intercept. This gives the condition that

$$e_{RC} < h_C + 1. \tag{3.17}$$

Note that in this case, the condition becomes

$$h_C + \frac{h_C}{h_{RC}} < e_{RC} < h_C + 1 \tag{3.18}$$

which implies that $h_C < h_{RC}$. This case gives either one, two, or three interior equilibria as shown in figure 3.1. Note that figures 3.1a and 3.1b each give us one interior equilibrium. In figure 3.1a, the consumer nullcline's horizontal asymptote is close to 1, so the consumer nullcline does not increase very rapidly. Therefore, the consumer nullcline does not intersect the resource nullcine until after the resource nullcline begins to decrease. On the other hand, in figure 3.1b, the consumer nullcline's horizontal asymptote is much greater than 1. So the consumer nullcline increases very rapidly and intersects the resource nullcline while the resource nullcline is still increasing.

(b) The resource nullcline's C-intercept is less than the consumer nullcline's
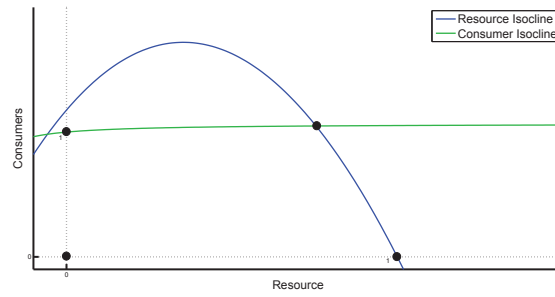
(a) $h_{RC} = 3.7,\ h_C = 0.05,\ e_{RC} = 0.9,\ r = 1.0,\ \alpha_{RC} = 0.25$
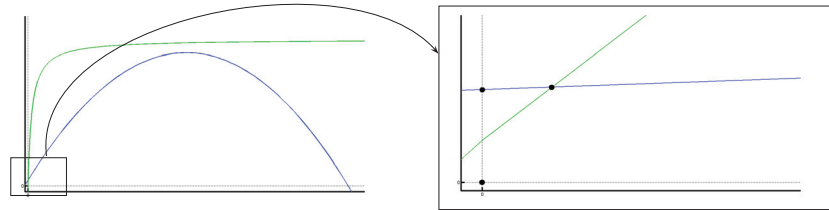
(b) $h_{RC} = 82.8,\ h_C = 0.00001,\ e_{RC} = 0.45,\ r = 0.1,\ \alpha_{RC} = 420.25$
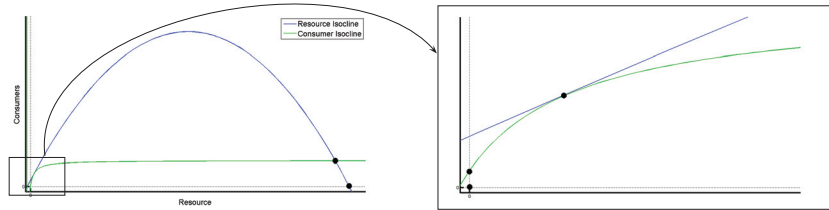
(c) $h_{RC} = 82.8,\ h_C = 0.00001,\ e_{RC} = 0.3333,\ r = 0.1,\ \alpha_{RC} = 80.25$
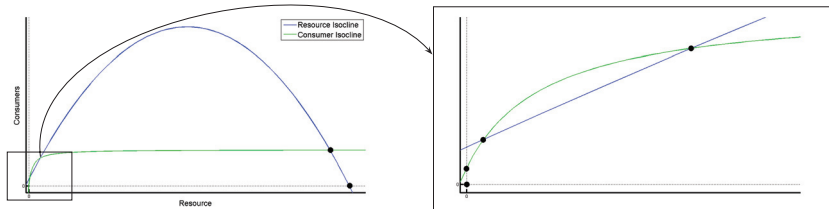
(d) $h_{RC} = 82.8,\ h_C = 0.00001,\ e_{RC} = 0.45,\ r = 0.1,\ \alpha_{RC} = 80.25$

Figure 3.1: *Case (1)(a), where the resource nullcline's vertical asymptote is less than the resource nullcline's R-intercept $R = -\frac{1}{h_{RC}}$, and the resource nullcline's C-intercept is greater than the consumer nullcline's C-intercept.*

C-intercept. This gives the condition that

$$e_{RC} > h_C + 1. \tag{3.19}$$

Note that in this case, the condition becomes

$$e_{RC} > \max\left(h_C + \frac{h_C}{h_{RC}}, h_C + 1\right) \tag{3.20}$$

Another way of saying this is

$$e_{RC} > h_C + \frac{h_C}{h_{RC}} \quad \text{if} \ \ h_C > h_{RC} \tag{3.21}$$

$$e_{RC} > h_C + 1 \ \ \text{if} \ \ h_C < h_{RC} \tag{3.22}$$

This case gives us either zero, one, or two interior equilibria as shown in figure 3.2.

(2) The resource nullcline's vertical asymptote is greater than the resource nullcline's R-intercept of $R = -\frac{1}{h_{RC}}$ but less than 0. This gives the condition that

$$h_C < e_{RC} < h_C + \frac{h_C}{h_{RC}}. \tag{3.23}$$

There are two subcases here.

(a) The resource nullcline's C-intercept is greater than the consumer nullcline's C-intercept. This gives us the condition that

$$e_{RC} < h_C + 1 \tag{3.24}$$
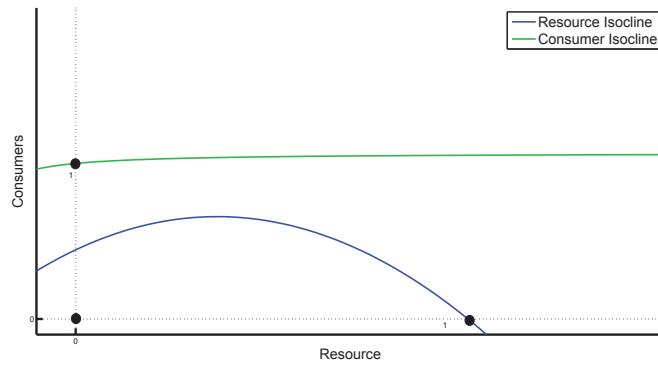
(a) $h_{RC} = 3.7$, $h_C = 0.05$, $e_{RC} = 2.3$, $r = 1.0$, $\alpha_{RC} = 0.25$
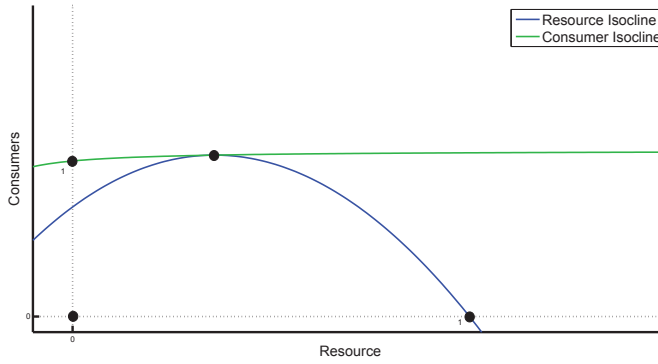
(b) $h_{RC} = 3.7$, $h_C = 0.05$, $e_{RC} = 1.47$, $r = 1.0$, $\alpha_{RC} = 0.25$
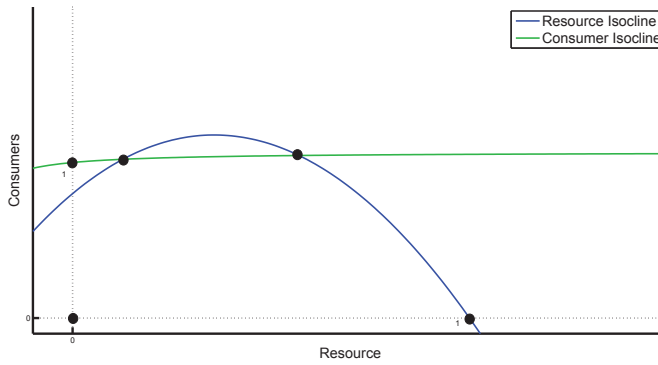
(c) $h_{RC} = 3.7$, $h_C = 0.05$, $e_{RC} = 1.3$, $r = 1.0$, $\alpha_{RC} = 0.25$

Figure 3.2: *Case (1)(b), where the resource nullcline's vertical asymptote is less than the resource nullcline's R-intercept $R = -\frac{1}{h_{RC}}$, and the resource nullcline's C-intercept is less than the consumer nullcline's C-intercept*
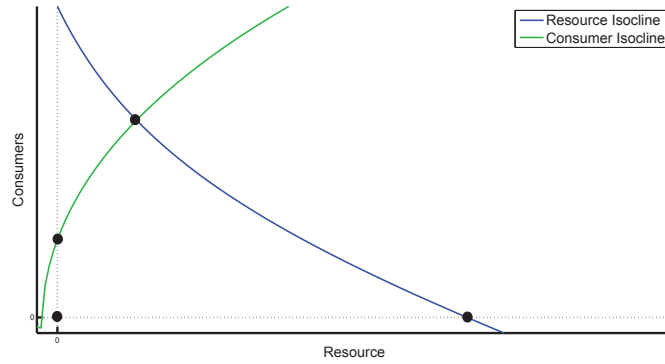
Figure 3.3: *Case (2)(a), where the resource nullcline's vertical asymptote is greater than the resource nullcline's R-intercept $R = -\frac{1}{h_{RC}}$ but less than 0, and the resource nullcline's C-intercept is greater than the consumer nullcline's C-intercept. Here the parameter values are $h_{RC} = 1.25$, $h_C = 0.75$, $e_{RC} = 1.0$, $r = 0.01$, $\alpha_{RC} = 0.25$*

Note that in this case, the condition becomes

$$h_C < e_{RC} < \min\left(h_C + \frac{h_C}{h_{RC}}, h_C + 1 \right) \tag{3.25}$$

Another way of saying this is

$$h_C < e_{RC} < h_C + \frac{h_C}{h_{RC}} \quad \text{if} \quad h_C < h_{RC} \tag{3.26}$$

$$h_C < e_{RC} < h_C + 1 \quad \text{if} \quad h_C > h_{RC} \tag{3.27}$$

This case gives us one interior equilibrium, as shown in figure 3.3.

(b) The resource nullcline's C-intercept is less than the consumer nullcline's C-intercept. This gives us the condition that

$$e_{RC} > h_C + 1 \tag{3.28}$$

Note that in this case, the condition becomes

$$h_C + 1 < e_{RC} < h_C + \frac{h_C}{h_{RC}} \tag{3.29}$$
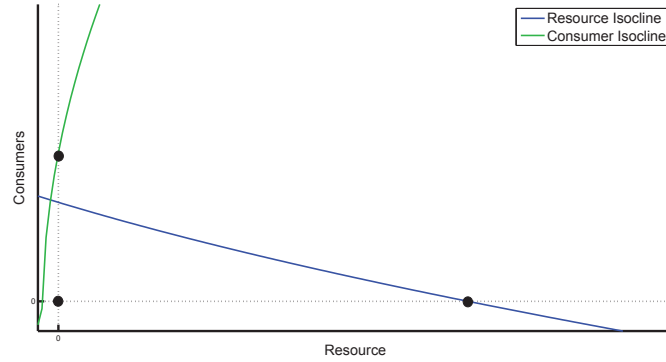
Figure 3.4: *Case (2)(b), where the resource nullcline's vertical asymptote is greater than the resource nullcline's R-intercept $R = -\frac{1}{h_{RC}}$ but less than 0, and the resource nullcline's C-intercept is less than the consumer nullcline's C-intercept. Here the parameter values are $h_{RC} = 0.25$, $h_C = 0.75$, $e_{RC} = 2.25$, $r = 0.01$, $\alpha_{RC} = 0.25$*
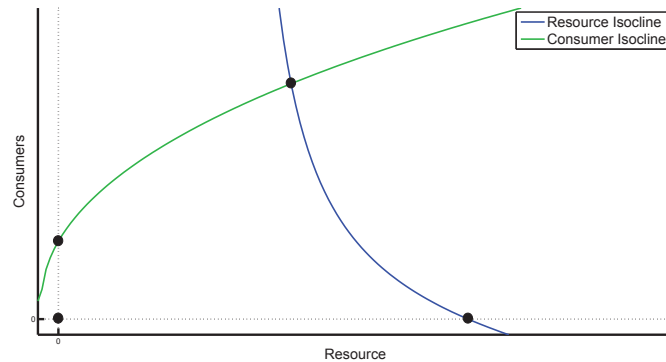
Figure 3.5: *Case (3), where the resource nullcline's vertical asymptote is greater than 0. Here the parameter values are $h_{RC} = 1.25$, $h_C = 1.75$, $e_{RC} = 1.0$, $r = 0.01$, $\alpha_{RC} = 0.25$*

which implies that $h_C > h_{RC}$. This case gives us no interior equilibria, as shown in figure 3.4.

(3) The resource nullcline's vertical asymptote is greater than 0. This gives us the condition that $e_{RC} < h_C$. This gives us one interior equilibrium, as shown in figure 3.5.

To get a better idea of when we might have interior equilibria and how many we might have, we note that $h(1) = \alpha_{RC} + e_{RC} + rh_{RC}e_{RC}^2 + re_{RC}^2 > 0$ and $h(0) = re_{RC}(e_{RC} - 1 - h_C) < 0$ if $\frac{1}{e_{RC} - h_C} > 1 \Leftrightarrow e_{RC} < h_C + 1$. In such a case, the

Intermediate Value Theorem guarantees $\exists\ R^* \in (0,1)$ such that $h\left(R^*\right) = 0$; i.e., if $e_{RC} < h_C + 1$ then there exists a solution to equation (3.12). Such is the case in cases (1)(a) and (2)(a).

We can also use Descartes' Rule of Signs, which tells us that in order to possibly be in the case where there are three interior equilibria, we must have three sign changes between a_3, a_2, a_1, and a_0. This requires the sign of each coefficient to change. Since $a_3 > 0$ for all biologically relevant parameter choices (i.e., all parameters are ≥ 0), then we must have $a_3 > 0$, $a_2 < 0$, $a_1 > 0$, and $a_0 < 0$. But $a_0 = re_{RC}\left(e_{RC} - 1 - h_C\right) < 0 \Leftrightarrow \frac{1}{e_{RC} - h_C} > 1 \Leftrightarrow e_{RC} < h_C + 1$.

From equation (3.13), we can determine conditions when C^* will be positive. It turns out that if $0 > -\frac{1}{h_{RC}} > 1 - \frac{e_{RC}}{h_C}$, as we have in cases (1)(a) and (1)(b), then $C^* > 0$ if $-\frac{1}{h_{RC}} < R^* < 1$. As noted above, the Intermediate Value Theorem guarantees that in case (1)(a) there exists an $R^* \in (0,1)$, so we know that in case (1)(a) we have at least one interior equilibrium. If $0 > 1 - \frac{e_{RC}}{h_C} > -\frac{1}{h_{RC}}$, as we have in case (2)(a) and (2)(b), then $C^* > 0$ provided that $1 - \frac{e_{RC}}{h_C} < R^* < 1$. As noted above, the Intermediate Value Theorem guarantees that in case (2)(a) there exists an $R^* \in (0,1)$, so we know that in case (2)(a) we have at least one interior equilibrium. If $1 - \frac{e_{RC}}{h_C} > 0 > -\frac{1}{h_{RC}}$, as we have in case (3), then $C^* > 0$ if $1 - \frac{e_{RC}}{h_C} < R^* < 1$.

In case (1)(b), we can see that there will be no interior equilibria if the maximum of the resource isocline is less than the consumer isocline's C-intercept and there will be two interior equilibria if the maximum of the resource isocline is greater than the consumer isocline's horizontal asymptote. If the resource isocline has a maximum, it occurs at

$$R_1 = \frac{2h_{RC}(e_{RC} - h_C) - \sqrt{4h_{RC}^2(e_{RC} - h_C)^2 + 4h_C h_{RC}(e_{RC}h_{RC} - h_C h_{RC} - e_{RC})}}{-2h_C h_{RC}}.$$

So if $f(R_1) < 1$ then there will be no interior equilibria in case (1)(b), and if $f(R_1) > 1 + \frac{\alpha_{RC}}{rh_{RC}}$ then there will be two interior equilibria in case (1)(b).

In case (1)(b), 2 interior equilibria coalesce into 1 then to 0, so there is a saddle-node bifurcation for e_{RC}.

3.3.2 Permanence

Theorem 3.7. *System (3.11) is dissipative.*

Proof. We have that $\frac{dR}{dt} \leq R(1 - R)$, so the resource equation is a lower solution to the logistic equation. Thus, $\forall \, \varepsilon > 0 \, \exists \, t_1 = t_1(R_0)$ such that $R < 1 + \varepsilon$ for $t \geq t_1$. In particular, there must be a t_1 such that $R(t) < 2 \, \forall \, t \geq t_1$. For $t \geq t_1$, the consumer equation is a lower solution to

$$\frac{dv}{dt} = rv(1 - v) + \frac{2\alpha_{RC}v}{1 + h_C v} \tag{3.30}$$

Equation (3.30) has two possible non-trivial equilibria:

$$v_1 = \frac{rh_C - r + \sqrt{r^2 h_C^2 + 2r^2 h_C + r^2 - 4\alpha_{RC} h_C}}{2rh_C} \tag{3.31}$$

$$v_2 = \frac{rh_C - r - \sqrt{r^2 h_C^2 + 2r^2 h_C + r^2 - 4\alpha_{RC} h_C}}{2rh_C} \tag{3.32}$$

This leads to three possibilities for the stability of the equilibria:

(i) If $r \leq 2\alpha_{RC}$ and $h_C \leq 1$ then $v_0 = 0$ is stable.

(ii) If $r > 2\alpha_{RC}$, or if $r = 2\alpha_{RC}$ and $h_C > 1$ then $v_0 = 0$ is unstable and $v_1 > 0$ is stable.

(iii) If $r < 2\alpha_{RC}$ and $h_C > 1$ then $v_0 = 0$ and $v_2 > 0$ are unstable while $v_1 > 0$ is stable.

For case (i), $C \to 0$ as $t \to \infty$, so $\forall \, \varepsilon > 0$ there exists ($\exists$) $t_2 = t_2(C_0)$ such that $C < \varepsilon$ for $t \geq t_2$. For cases (ii) and (iii), $\forall \, \varepsilon > 0 \, \exists \, t_3 = t_3(C_0)$ such that $C < v_1 + \varepsilon$ for $t \geq t_3$.

Thus, in either case, $\exists\, t_C(C_0) = \max(t_2, t_3)$ such that $C < v_1 + \varepsilon$ for $t \geq t_C$. So, there is a $t_* > 0$ such that

$$R < 1 + \varepsilon$$

$$C < v_1 + \varepsilon$$

for $t \geq t_*$. Thus, the system (3.11) is dissipative. $\qquad\square$

Theorem 3.8. *System (3.11) is permanent if*

$$e_{RC} < h_C + 1. \tag{3.33}$$

Proof. To establish permanence, all that remains is to check the invasibility condition near each equilibrium. Linearizing the resource equation in system (3.11) about $(0, 0)$ gives

$$\frac{dR}{dt} = R.$$

Since the intrinsic growth rate is $1 > 0$, R can invade C when $C = 0$.

The linearization of the consumer equation in system (3.11) about $(0, 0)$ gives

$$\frac{dC}{dt} = rC.$$

Since the intrinsic growth rate is $r > 0$, C can invade R when $R = 0$.

The linearization of the consumer equation in (3.11) about $(1, 0)$ gives

$$\frac{dC}{dt} = \left(r + \frac{\alpha_{RC}}{1 + h_{RC}}\right)C.$$

Since the intrinsic growth rate is $r + \frac{\alpha_{RC}}{1 + h_{RC}} > 0$, C can invade R when R is at its carrying capacity of $R = 1$.

Linearizing the resource equation in (3.11) about $(0, 1)$ gives

$$\frac{dR}{dt} = \left(1 - \frac{e_{RC}}{1 + h_C}\right) C.$$

Because of inequality (3.33), the intrinsic growth rate is $1 - \frac{e_{RC}}{1+h_C} > 0$. Thus, R can invade C when C is at its carrying capacity of $C = 1$. □

3.3.3 Local Stability

The local stability of the boundary equilibria is given by the following.

Theorem 3.9. *With regards to local stability of the boundary equilibria, the following hold.*

(i) $(0, 0)$ is an unstable node.

(ii) $(1, 0)$ is a saddle.

(iii) $(0, 1)$ is a saddle if (3.33) holds and a stable node if (3.33) is reversed.

Note that system (3.11) is permanent if (3.33) holds. But (3.33) is exactly the condition required for $(0, 1)$ to be a saddle, in which case an interior equilibrium will exist. So the system is not permanent if $(0, 1)$ is a stable node.

Proof. The Jacobian matrix J for system (3.11) is

$$J(R, C) = \begin{pmatrix} 1 - 2R - \frac{h_C e_{RC} C^2 + e_{RC} C}{(1 + h_{RC} R + h_C C)^2} & -\frac{h_{RC} e_{RC} R^2 + e_{RC} R}{(1 + h_{RC} R + h_C C)^2} \\ \\ \frac{h_C \alpha_{RC} C^2 + \alpha_{RC} C}{(1 + h_{RC} R + h_C C)^2} & r - 2rC + \frac{\alpha_{RC} h_{RC} R^2 + \alpha_{RC} R}{(1 + h_{RC} R + h_C C)^2} \end{pmatrix}. \qquad (3.34)$$

(i) The Jacobian of the linearization of (3.11) about $(0, 0)$ is

$$J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & r \end{pmatrix}.$$

The eigenvalues are then $\lambda_1 = 1 > 0$ and $\lambda_2 = r > 0$. Since this has two positive eigenvalues, $(0,0)$ is an unstable node.

(ii) The Jacobian of the linearization of (3.11) about $(1,0)$ is

$$J(1,0) = \begin{pmatrix} -1 & -\frac{e_{RC}}{1+h_{RC}} \\ 0 & r + \frac{\alpha_{RC}}{1+h_{RC}} \end{pmatrix}.$$

The eigenvalues are then $\lambda_1 = -1 < 0$ and $\lambda_2 = r + \frac{\alpha_{RC}}{1+h_{RC}} > 0$. Since there is one positive eigenvalue and one negative eigenvalue, $(1,0)$ is a saddle.

(iii) The Jacobian of the linearization of (3.11) about $(0,1)$ is

$$J(0,1) = \begin{pmatrix} 1 - \frac{e_{RC}}{1+h_C} & 0 \\ \frac{\alpha_{RC}}{1+h_C} & -r \end{pmatrix}.$$

The eigenvalues are then $\lambda_1 = -r < 0$ and $\lambda_2 = 1 - \frac{e_{RC}}{1+h_C}$. The sign on λ_2 depends on the value of e_{RC} relative to the value of $h_C + 1$. If $e_{RC} < h_C + 1$; i.e., if (3.33) holds, then $\lambda_2 > 0$ and there is one positive eigenvalue and one negative eigenvalue. In this case, $(0,1)$ is a saddle. If $e_{RC} > h_C + 1$; i.e., if (3.33) is reversed, then $\lambda_2 < 0$ and there are two negative eigenvalues. In this case, $(0,1)$ is a stable node.

$\square$

Determining the local stability of an interior equilibrium $E^* = (R^*, C^*)$ in the conventional manner, as was done with the boundary equilibria, leads to prohibitively messy calculations. Nevertheless, we can try to determine the stability properties by first constructing a rectangular region Ω about E^* which is compact and studying the direction of the flow of the system along $\partial\Omega$. We will then show that Ω can be made arbitrarily close to E^*, which will eliminate the possibility of having limit cycles
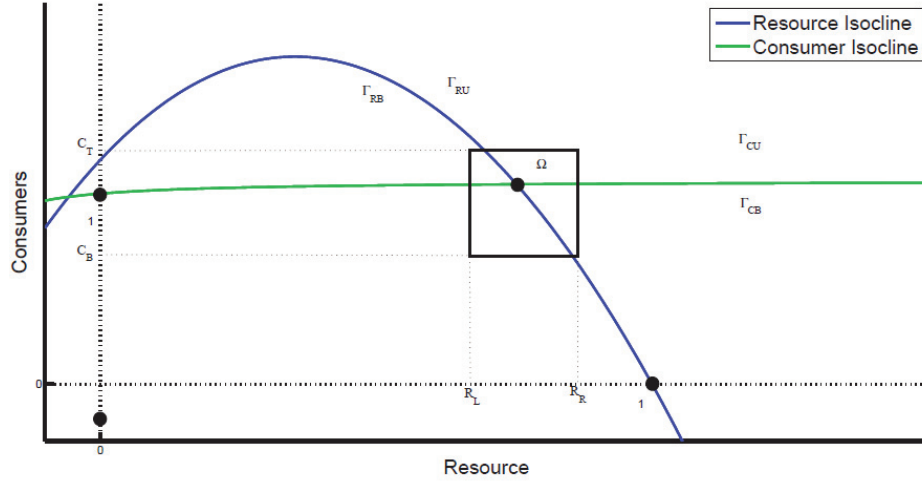
Figure 3.6: *The rectangular region Ω in case (1)(a) when there is one interior equilibrium.*

within Ω.

Before defining Ω, we note that the resource isocline divides $\mathbb{R}^2_{\geq 0}$ into two regions: one region, Γ_{RB}, which is bounded by the R-axis, the C-axis, and the resource isocline, and its complement, Γ_{RU}, which contains values of R which are unbounded. Similarly, the consumer isocline divides $\mathbb{R}^2_{\geq 0}$ into two regions: one region, Γ_{CB}, which is bounded by the R-axis, C-axis, and the consumer isocline (though it contains unbounded values of R), and its complement, Γ_{CU}, which contains unbounded values of C.

We define Ω by $\Omega = \{(R, C) : (R, C) \in [R_L, R_R] \times [C_B, C_T]\}$ for some values R_L, R_R, C_B, C_T. We will require that the left side of Ω, $\mathcal{L} = \{R_L\} \times [C_B, C_T]$ and the right side of Ω, $\mathcal{R} = \{R_R\} \times [C_B, C_T]$, be entirely contained (except possibly at their endpoints which we allow to be on the isoclines) on opposite sides of the resource isocline; i.e., either $\mathcal{L} \subset \Gamma_{RB}$ while $\mathcal{R} \subset \Gamma_{RU}$ or $\mathcal{L} \subset \Gamma_{RU}$ while $\mathcal{R} \subset \Gamma_{RB}$. Similarly, we will require the top of Ω, $\mathcal{T} = [R_L, R_R] \times \{C_T\}$ and the bottom of Ω, $\mathcal{B} = [R_L, R_R] \times \{C_B\}$ to be entirely contained (except possibly at their endpoints which we allow to be on the isoclines) on opposite sides of the consumer isocline; i.e., $\mathcal{T} \subset \Gamma_{CB}$ while $\mathcal{B} \subset \Gamma_{CU}$. We show a typical Ω in Figure (3.6) for case (1)(a) when there is one interior equilibrium.

To determine the direction of the flow along $\mathcal{L}$ and $\mathcal{R}$, we need to determine the sign of $\frac{dR}{dt} = R\left[1 - R - \frac{e_{RC}C}{1+h_{RC}R+h_C C}\right]$. Since we must have $R \geq 0$, this amounts to determining the sign of $1 - R - \frac{e_{RC}C}{1+h_{RC}R+h_C C}$. To determine the direction of the flow along $\mathcal{T}$ and $\mathcal{B}$, we need to determine the sign of $\frac{dC}{dt} = C\left[r(1-C) + \frac{\alpha_{RC}R}{1+h_{RC}R+h_C C}\right]$. Since we must have $C \geq 0$, this amounts to determining the sign of $r(1-C) + \frac{\alpha_{RC}R}{1+h_{RC}R+h_C C}$.

Lemma 3.10. *Along $\mathcal{T} \subset \Gamma_{CU}$, $\frac{dC}{dt} < 0$.*

Proof. First let us consider the case where $\mathcal{T}$ lies entirely above the consumer isocline's horizontal asymptote; i.e., $C_{\mathcal{T}} > 1 + \frac{\alpha_{RC}}{rh_{RC}}$. Then we have that $C > 1 + \frac{\alpha_{RC}}{rh_{RC}}$ which implies that $-rC < -r - \frac{\alpha_{RC}}{h_{RC}}$. So,

$$
\begin{aligned}
r - rC + \frac{\alpha_{RC}R}{1+h_{RC}R+h_C C} &< r - r - \frac{\alpha_{RC}}{h_{RC}} + \frac{\alpha_{RC}R}{1+h_{RC}R+h_C C} \\
&= -\frac{\alpha_{RC}}{h_{RC}} + \frac{\alpha_{RC}R}{1+h_{RC}R+h_C C} \\
&< -\frac{\alpha_{RC}}{h_{RC}} + \frac{\alpha_{RC}R}{1+h_{RC}R} \\
&= \frac{-\alpha_{RC}\left(1+h_{RC}R\right) + h_{RC}\alpha_{RC}R}{h_{RC}\left(1+h_{RC}R\right)} \\
&= -\frac{\alpha_{RC}}{h_{RC}\left(1+h_{RC}R\right)} \\
&< 0
\end{aligned}
$$

So, along $\mathcal{T}$, $\frac{dC}{dt} < 0$ when $\mathcal{T}$ lies entirely above the consumer isocline's horizontal asymptote.

But by the definition of isocline, we must also have that $\frac{dC}{dt} < 0$ along $\mathcal{T}$, even when $\mathcal{T}$ is not above the consumer isocline's horizontal asymptote. So, as long as $\mathcal{T} \subset \Gamma_{CU}$, then $\frac{dC}{dt} < 0$. $\qquad\square$

Lemma 3.11. *Along $\mathcal{B} \subset \Gamma_{CB}$, $\frac{dC}{dt} > 0$.*

Proof. Let us first consider the case where $C_{\mathcal{B}} < 1$. We have that $r(1-C) +$

$\frac{\alpha_{RC}R}{1+h_{RC}R+h_C C} > r(1-C)$. If $C_B < 1$ then $r(1-C) > 0$. Thus, along $\mathcal{B}$, we have that $\frac{dC}{dt} > 0$ provided that $C_B < 1$.

But as before, the definition of isocline implies that we must have $\frac{dC}{dt} > 0$ along $\mathcal{B}$, even when $C_B > 1$. So, as long as $\mathcal{B} \subset \Gamma_{CB}$, then $\frac{dC}{dt} > 0$. $\qquad\square$

Lemma 3.12. *Along the side contained in* Γ_{RU}, $\frac{dR}{dt} < 0$.

Proof. First note that $1 - R - \frac{e_{RC}C}{1+h_{RC}R+h_C C} < 1 - R$. We know that $R^* < 1$. In the case where $R_R > 1$, we have that $1 - R < 0$ so that $\frac{dR}{dt} < 0$ along the side within Γ_{CU}.

But again, the definition of isocline ensure that $\frac{dR}{dt} < 0$, even when R_R is not greater than 1. So, along the side within Γ_{RU}, $\frac{dR}{dt} < 0$. $\qquad\square$

Lemma 3.13. *Along the side within* Γ_{RB}, $\frac{dR}{dt} > 0$.

Proof. Note that $\lim\limits_{R,C \to 0} \left(1 - R - \frac{e_{RC}C}{1+h_{RC}R+h_C C}\right) = 1$. Therefore, $\exists \ \varepsilon_R, \varepsilon_C > 0$ such that $R < \varepsilon_R$ and $C < \varepsilon_C \Rightarrow 1 - R - \frac{e_{RC}C}{1+h_{RC}R+h_C C} > 0$; i.e., such that $\frac{dR}{dt} > 0$.

Once more, the definition of isocline tells us that $\frac{dR}{dt} > 0$, even when $C > \varepsilon_C$ and $\frac{dR}{dt} > 0$ along the side within Γ_{CB}, even when $R > \varepsilon_R$. So, along the side within Γ_{RB}, $\frac{dR}{dt} > 0$. $\qquad\square$

So far we have shown that any Ω we can construct with $\mathcal{T} \subset \Gamma_{CU}, \mathcal{B} \subset \Gamma_{CB}, \mathcal{L} \subset \Gamma_{RB}, \mathcal{R} \subset \Gamma_{RU}$, or $\mathcal{T} \subset \Gamma_{CU}, \mathcal{B} \subset \Gamma_{CB}, \mathcal{L} \subset \Gamma_{RU}, \mathcal{R} \subset \Gamma_{RB}$, will be such that $\frac{dC}{dt} < 0$ along $\mathcal{T}$, $\frac{dC}{dt} > 0$ along $\mathcal{B}$, $\frac{dR}{dt} < 0$ along the side within Γ_{RU}, and $\frac{dR}{dt} > 0$ along the side within Γ_{RB}. Next we need to show that we can construct Ω with sides arbitrarily close to a given E^*. To this end, we have the following lemma.

Lemma 3.14. *Let* $\varepsilon_T > 0$, $\varepsilon_L > 0$, $\varepsilon_B > 0$, *and* $\varepsilon_R > 0$ *be given. Then we can construct a rectangular region* Ω *with the properties described prior to Lemma 3.10 such that* $d\left(\mathcal{T}, C^*\right) \le \varepsilon_T$, $d\left(\mathcal{L}, R^*\right) \le \varepsilon_L$, $d\left(\mathcal{B}, C^*\right) \le \varepsilon_B$, *and* $d\left(\mathcal{R}, R^*\right) \le \varepsilon_R$.

Proof. We start with Case 1, where the resource nullcline's vertical asymptote is less than the resource nullcline's R-intercept. Assume that E^* is to the right of the R-value where the resource isocline attains its maximum value.

Note that in this case, $\frac{\partial f}{\partial R} < 0$ so f will cross into Ω either through $\mathcal{T}$ to the left of E^* or through $\mathcal{L}$ above E^*, and will cross out of Ω either through $\mathcal{B}$ to the right of E^* or through $\mathcal{R}$ below E^*. In order for Ω to have the properties described prior to Lemma 3.10, namely that $\mathcal{L}$ and $\mathcal{R}$ remain entirely on one side of the resource isocline, we cannot have f cross into Ω through $\mathcal{L}$ above E^* or out of Ω through $\mathcal{R}$ below E^*. In order to ensure that f will cross into Ω through $\mathcal{T}$ to the left of E^*, we will need to make sure that the maximum value of R_L is the location where the resource isocline intersects the line $C = C_T$ or the maximum value of C_T is the location where the resource isocline intersects the line $R = R_L$. Since we will want to be able to make the sides of Ω arbitrarily close to E^*, we will make sure the maximum value of C_T the location where the resource isocline intersects the line $R = R_L$. Likewise, in order for f to cross out of Ω through $\mathcal{B}$ to the right of E^*, we must have that the minimum value of R_R is the location where the resource isocline intersects the line $C = C_B$ or the maximum value of C_B is the location where the resource isocline intersects the line R_R. In order for the sides of Ω to be made arbitrarily close to E^*, we will make sure the minimum value of C_B is the location where the resource isocline intersects the line R_R.

Similarly, $\frac{\partial g}{\partial R} > 0$ in this case, so g will cross into Ω either through $\mathcal{B}$ to the left of E^* or through $\mathcal{L}$ below E^*, and will cross out of Ω either through $\mathcal{T}$ to the right of E^* or through $\mathcal{R}$ above E^*. In order for $\mathcal{T}$ and $\mathcal{B}$ to remain entirely on one side of the consumer isocline, both requirements for Ω, g cannot cross into Ω through $\mathcal{B}$ to the left of E^* or out of Ω through $\mathcal{T}$ to the right of E^*. In order to ensure that g will cross into Ω through $\mathcal{L}$ below E^*, we will need to make sure that the minimum value of R_L is the location where the consumer isocline intersects the line $C = C_B$ or the maximum value of C_B is the location where the consumer isocline intersects the line $R = R_L$. In order to be able to make the sides of Ω as close to E^* as we would like, we will need the minimum value of R_L to be the location where the consumer

isocline intersects the line $C = C_B$. Likewise, in order for g to cross out of Ω through $\mathcal{R}$ above E^*, we must have that the maximum value of R_R is the location where the consumer isocline intersects the line $C = C_T$ or the minimum value of C_T is the location where the resource isocline intersects the line $R = R_R$. In order to have the sides of Ω arbitrarily close to E^*, we need to make sure the maximum value of R_R is the location where the consumer intersects the line $C = C_T$.

Now, we make the following notational definitions:

$$P_R = \left\{(R,C) : R = R^* + \varepsilon_R\right\} \cap \left\{(R,C) : C = f(R)\right\}$$

$$P_B = \left\{(R,C) : C = C^* - \varepsilon_B\right\} \cap \left\{(R,C) : C = g(R)\right\}$$

$$P_L = \left\{(R,C) : R = R^* - \varepsilon_L\right\} \cap \left\{(R,C) : C = f(R)\right\}$$

$$P_T = \left\{(R,C) : C = C^* + \varepsilon_T\right\} \cap \left\{(R,C) : C = g(R)\right\}$$

Let $d = \min\{d_R, d_B, d_L, d_T\}$, where

$$d_R = d\left(P_R, \left\{(R,C) : C = C^*\right\}\right)$$

$$d_B = d\left(P_B, \left\{(R,C) : R = R^*\right\}\right)$$

$$d_L = d\left(P_L, \left\{(R,C) : C = C^*\right\}\right)$$

$$d_T = d\left(P_T, \left\{(R,C) : R = R^*\right\}\right)$$

Suppose that d is realized at the point $P_i = \left(\tilde{R}_i, \tilde{C}_i\right)$ ($i = R, B, L$, or T). If $i = T$ (or B) then we begin by constructing Ω by letting $R_R = \min\left\{\tilde{R}_T, R^* + \varepsilon_R\right\}$ (or $R_L = \max\left\{\tilde{R}_B, R^* - \varepsilon_L\right\}$, respectively). If $i = R$ (or L) then we begin constructing Ω by letting $C_B = \max\left\{\tilde{C}_R, C^* - \varepsilon_B\right\}$ (or $C_T = \min\left\{\tilde{C}_T, C^* + \varepsilon_T\right\}$, respectively). We then proceed to construct the remaining sides of Ω in clockwise order by letting

the next two sides be determined as follows:

$$R_L = \max\left\{R^* - \varepsilon_L, \{(R,C) : C = f(R)\} \cap \{(R,C) : C = C_B\}\right\}$$

$$C_T = \min\left\{C^* + \varepsilon_T, \{(R,C) : C = g(R)\} \cap \{(R,C) : R = R_L\}\right\}$$

$$R_R = \min\left\{R^* + \varepsilon_R, \{(R,C) : C = f(R)\} \cap \{(R,C) : C = C_T\}\right\}$$

$$C_B = \max\left\{C^* - \varepsilon_B, \{(R,C) : C = g(R)\} \cap \{(R,C) : R = R_R\}\right\}$$

If the last side of Ω is $\mathcal{R}$, we let $R_R = \min\left\{R^* + \varepsilon_R, \tilde{R}_T\right\}$. If the last side of Ω is $\mathcal{B}$, we let $C_B = \max\left\{C^* - \varepsilon_B, \tilde{C}_R\right\}$. If the last side of Ω is $\mathcal{L}$, we let $R_L = \max\left\{R^* - \varepsilon_L, \tilde{R}_B\right\}$. And if the last side of Ω is $\mathcal{T}$, we let $R_T = \min\left\{R^* = \varepsilon_T, \tilde{R}_L\right\}$. This will give us Ω with the desired properties.

Now we assume that E^* is to the left of the R-value where the resource isocline attains its maximum value.

Note that in this case, $\frac{\partial f}{\partial R} > 0$ so f will cross into Ω either through $\mathcal{B}$ to the left of E^* or through $\mathcal{L}$ below E^*, and will cross out of Ω either through $\mathcal{T}$ to the right of E^* or through $\mathcal{R}$ above E^*. In order for Ω to have the properties described prior to Lemma 3.10, namely that $\mathcal{L}$ and $\mathcal{R}$ remain entirely on one side of the resource isocline, we cannot have f cross into Ω through $\mathcal{L}$ below E^* or out of Ω through $\mathcal{R}$ above E^*. In order to ensure that f will cross into Ω through $\mathcal{B}$ to the left of E^*, we will need to make sure the maximum value of R_L is the location where the resource isocline intersects the line $C = C_B$ or the minimum value of C_B is the location where the resource isocline intersects the line $R = R_L$. Since we will want to be able to make the sides of Ω arbitrarily close to E^*, we will make sure the minimum value of C_B is the location where the resource isocline intersects the line $R = R_L$. Likewise, in order for f to cross out of Ω through $\mathcal{T}$ to the right of E^*, we must have that

the minimum value of R_R is the location where the resource isocline intersects the line $C = C_T$ or the maximum value of C_T is the location where the resource isocline intersects the line $R = R_R$. In order to be able to make the sides of Ω as close to E^* as we want, we will make sure the maximum value of C_T is the location where the resource isocline intersects the line $R = R_R$.

Similarly, $\frac{\partial g}{\partial R} > 0$ in this case, so g will cross into Ω either through $\mathcal{L}$ below E^* or through $\mathcal{B}$ to the left of E^*, and will cross out of Ω either through $\mathcal{R}$ above E^* or through $\mathcal{T}$ to the right of E^*. In order for $\mathcal{T}$ and $\mathcal{B}$ to remain entirely on one side of the consumer isocline, both requirements for Ω, g cannot cross into Ω through $\mathcal{B}$ to the left of E^* or out of Ω through $\mathcal{T}$ to the right of E^*. In order to ensure that g will cross into Ω through $\mathcal{L}$ below E^*, we will need to make sure that the minimum value of R_L is the location where the consumer isocline intersect the line $C = C_B$ or the maximum value of C_B is the location where the consumer isocline intersects the line $R = R_L$. Since we will want to make the sides of Ω arbitrarily close to E^*, we will make sure the minimum value of R_L is the location where the consumer isocline intersects the line $C = C_B$. Likewise, in order for g to cross out of Ω through $\mathcal{R}$ above E^*, we must have that the maximum value of R_R is the location where the consumer isocline intersects the line $C = C_T$ or the minimum value of C_T is the location where the consumer isocline intersects the line $R = R_R$. In order to be able to make the sides of Ω as close to E^* as we want, we will need the maximum value of R_R is the location where the consumer isocline intersects the line $C = C_T$.

$\underline{\text{Claim}}$: If $\frac{\partial f}{\partial R} < \frac{\partial g}{\partial R}$, then one of the following must be true:

(a) f crosses through $\mathcal{R}$ above E^*

(b) g crosses through $\mathcal{T}$ to the right of E^*.

Note that this will guarantee that Ω cannot be constructed as described prior to Lemma 3.10 with sides arbitrarily close to E^*.

Proof of claim: If the consumer isocline crosses out of Ω through $\mathcal{T}$ then we are done. So suppose that the consumer isocline does not cross through $\mathcal{T}$. Then the maximum possible value of R_R, $R_{R,max}$, is the location where the consumer isocline intersects the line $C = C_T$. But since $0 < \frac{\partial f}{\partial R} < \frac{\partial g}{\partial R}$, the R-value where the resource isocline intersects the line $C = C_T$ would have to be greater than $R_{R,max}$, so the resource isocline does not cross out of Ω through $\mathcal{T}$. Thus, the resource isocline crosses out of Ω through $\mathcal{R}$.

A similar proof shows that either the resource isocline crosses through $\mathcal{L}$ below E^* or the consumer isocline crosses through $\mathcal{B}$ to the left of E^*. So in order to be able to construct Ω as desired, we need $\frac{\partial f}{\partial R} > \frac{\partial g}{\partial R}$, which we assume to be the case in what follows.

Let P_i ($i = R, B, L$, or T) be defined as earlier in this proof. Then we construct Ω by first letting $R_R = \min\{P_T, R^* + \varepsilon_R\}$. Next we let $C_T = \min\{C^* + \varepsilon_T, \{(R,C) : R = R_R\} \cap \{(R,C) : g(R) = 0\}\}$. We then let $R_L = \max\{R^* - \varepsilon_L, \{(R,C) : C = C^* - \varepsilon_B\} \cap \{(R,C) : g(R) = 0\}\}$. Finally we let $C_B = \max\{C^* - \varepsilon_B, \{(R,C) : R = R_L\} \cap \{(R,C) : f(R) = 0\}\}$. This will give us Ω with the desired properties.

If we are is Cases 2 or 3, $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$, so the proof proceeds the same as in Case 1 with E^* to the right of the R-value where the resource isocline attains its maximum value. $\square$

Thus, we have proved the following theorem.

Theorem 3.15. *If*

1. $\frac{\partial f}{\partial R} < 0$ *and* $\frac{\partial g}{\partial R} > 0$ *then* E^* *is locally stable node.*

2. $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, *and* $\frac{\partial f}{\partial R} > \frac{\partial g}{\partial R}$ *then* E^* *is a saddle.*

3. $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, *and* $\frac{\partial g}{\partial R} > \frac{\partial f}{\partial R}$ *then we cannot construct* Ω *around* E^*.

Before we state the local stability of each interior equilibrium point, let us introduce the following notation.

1. In case (1)(a), when there are three interior equilibria, we will denote the interior equilibria by E_i, where $i = 1, 2, 3$ and where the R-value of E_1 is less than the R-value of E_2, which is less than the R-value of E_3. In case (1)(b), when there are two interior equilibria, we will denote the interior equilibria in a similar fashion.

2. The R-value where the resource isocline attains its maximum value will be denoted by R_{max}.

3. The right hand side of the resource equation in system (3.11) will be represented by $F(R, C)$ and the right hand side of the consumer equation in system (3.11) will be represented by $G(R, C)$.

4. We will let $\delta = \frac{\partial F}{\partial C} \frac{\partial G}{\partial R} \left(\frac{f'(R)}{g'(R)} - 1 \right)$ and $\tau = - \left[\frac{\partial F}{\partial C} f'(R) + \frac{\frac{\partial G}{\partial R}}{g'(R)} \right]$.

Theorem 3.16.   *1. In case (1)(a), when there is one interior equilibrium which is to the right of R_{max}, E^* is a stable node.*

2. In case (1)(a), when there is one interior equilibrium which is to the left of R_{max}, E^* could be a node, focus, or center. In case (1)(a), when there are three interior equilibria, E_1^* could be a node, focus, or center, E_2 is a saddle, and E_3 is a stable node. E^* or E_1 will be a node if $\tau^2 - 4\delta \geq 0$, a focus if $\tau^2 - 4\delta < 0$ and $\tau \neq 0$, and will need further investigation if $\tau = 0$. E^* or E_1 will be stable if $\tau < 0$ and unstable if $\tau > 0$.

3. In case (1)(b), when there are two interior equilibria, E_1 is a saddle and E_2 is a stable node.

4. In case (2)(a), when there is one interior equilibrium, and in case (3), the interior equilibrium E^* is a stable node.

Proof. 1. In case (1)(a), when there is one interior equilibrium which is to the right of R_{max}, we have $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$. So by part (i) of theorem (3.15), we have that E^* is a stable node.

2. In case (1)(a), when there are three interior equilibria, we have that $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, and $\frac{\partial f}{\partial R} > \frac{\partial g}{\partial R}$ at E_2, and $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$ at E_3. So by parts (ii) and (i), respectively, of theorem (3.15), E_2 is a saddle and E_3 is a stable node. At E^*, in the case where there is one interior equilibrium which is to the left of R_{max}, or at E_1, in the case where there are three interior equilibria, we have $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, and $\frac{\partial g}{\partial R} > \frac{\partial f}{\partial R}$. So by part (iii) of theorem (3.15), we cannot construct Ω around E^* or E_1^* to determine local stability.

But, the resource isocline is given by $F(R,C) = 0 \Leftrightarrow C = f(R)$. Similarly, the consumer isocline is given by $G(R,C) = 0 \Leftrightarrow C = g(R)$. So differentiating both equations with respect to R gives us $\frac{\partial F}{\partial R} + \frac{\partial F}{\partial C}f'(R) = 0$ and $\frac{\partial G}{\partial R} + \frac{\partial G}{\partial C}g'(R) = 0$. Using these in the Jacobian gives us

$$
J = \begin{pmatrix} \frac{\partial F}{\partial R} & \frac{\partial F}{\partial C} \\ \frac{\partial G}{\partial R} & \frac{\partial G}{\partial C} \end{pmatrix} = \begin{pmatrix} -\frac{\partial F}{\partial C}f'(R) & \frac{\partial F}{\partial C} \\ \frac{\partial G}{\partial R} & -\frac{\frac{\partial G}{\partial R}}{g'(R)} \end{pmatrix}.
$$

It is easy to see that $\delta = \det(J)$ and $\tau = \text{tr}(J)$. To determine the sign of δ, we first note that $\frac{\partial F}{\partial C} < 0$ and $\frac{\partial G}{\partial R} > 0$. Since we are in the case where $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, and $\frac{\partial g}{\partial R} > \frac{\partial f}{\partial R}$, then we have that $\delta > 0$. Therefore, we have that E^* or E_1 will be a node if $\tau^2 - 4\delta \geq 0$ and a focus if $\tau^2 - 4\delta < 0$ and $\tau \neq 0$. If $\tau = 0$ then linearly we have a center, but in the nonlinear case, we need to investigate further by looking at higher order terms. E^* or E_1 will be stable if $\tau < 0$ and unstable if $\tau > 0$.

3. In case (1)(b), when there are two interior equilibria, we have $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, and $\frac{\partial f}{\partial R} > \frac{\partial g}{\partial R}$ at E_1, and $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$ at E_2. So by parts (ii) and (i),

respectively, of theorem (3.15), E_1 is a saddle and E_2 is a stable node.

4. In case (2)(a), when there is one interior equilibrium, and in case (3), we have $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$. So by part (i) of theorem (3.15), E^* is a stable node.

Remark: The conclusions of theorem (3.15) are consistent with the analysis of E_1 is part (ii) of theorem (3.16). To see this, note that if $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$ then $\delta > 0$. Also in this case, $\tau < 0$. So $\frac{\partial f}{\partial R} < 0$ and $\frac{\partial g}{\partial R} > 0$ implies than E^* is a stable node provided $\tau^2 - 4\delta \geq 0$. Similarly, if $\frac{\partial f}{\partial R} > 0$, $\frac{\partial g}{\partial R} > 0$, and $\frac{\partial f}{\partial R} > \frac{\partial g}{\partial R}$ then $\delta < 0$ so E^* is a saddle. $\qquad\square$

3.3.4 Global Stability

Theorem 3.17. *The non-trivial equilibrium (R^*, C^*) is globally asymptotically stable whenever it exists, provided $h_{RC} < \frac{1}{1-R^*}$ $\left(\text{or equivalently } R^* > 1 - \frac{1}{h_{RC}}\right)$.*

Proof. Let $V_1(R) = R - R^* - R^* \ln\left(\frac{R}{R^*}\right)$ and $V_2(C) = C - C^* - C^* \ln\left(\frac{C}{C^*}\right)$. Then $V(R, C) = V_1(R) + \beta V_2(C)$ is a Lyapunov function. To compute $\frac{\partial V}{\partial t}$, we first need $\frac{dV_1(R)}{dt}$ and $\frac{dV_2(C)}{dt}$. To this end, we have

$$
\begin{aligned}
\frac{dV_1(R)}{dt} &= \frac{dV_1}{dR}\frac{dR}{dt} \\
&= \left[1 - R^*\left(\frac{R^*}{R}\right)\frac{1}{R^*}\right]\left[R(1-R) - \frac{e_{RC}CR}{1 + h_{RC}R + h_C C}\right] \\
&= (R - R^*)\left[1 - R - \frac{e_{RC}C}{1 + h_{RC}R + h_C C}\right]
\end{aligned}
$$

If (R^*, C^*) exists then R^* and C^* must satisfy

$$
\begin{aligned}
0 &= R^*\left(1 - R^*\right) - \frac{e_{RC}C^*R^*}{1 + h_{RC}R^* + h_C C^*} \\
\Rightarrow 0 &= 1 - R^* - \frac{e_{RC}C^*}{1 + h_{RC}R^* + h_C C^*} \\
\Leftrightarrow 1 &= R^* + \frac{e_{RC}C^*}{1 + h_{RC}R^* + h_C C^*}
\end{aligned}
$$

Thus,

$$
\begin{aligned}
\frac{dV_1(R)}{dt} =& \left(R - R^*\right)\left[R^* - R + \frac{e_{RC}C^*}{1 + h_{RC}R^* + h_C C^*} - \frac{e_{RC}C}{1 + h_{RC}R + h_C C}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right) \\
& \left[\frac{e_{RC}C^*\left(1 + h_{RC}R + h_C C\right) - e_{RC}C\left(1 + h_{RC}R^* + h_C C^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right)\left[\frac{e_{RC}C^* + e_{RC}h_{RC}C^*R - e_{RC}C - e_{RC}h_{RC}CR^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right) \\
& \left[\frac{e_{RC}C^* + e_{RC}h_{RC}C^*R - e_{RC}C - e_{RC}h_{RC}CR^* + e_{RC}h_{RC}C^*R^* - e_{RC}h_{RC}C^*R^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right) \\
& \left[\frac{\left(e_{RC}h_{RC}C^*R - e_{RC}h_{RC}C^*R^*\right) + \left(e_{RC}C^* - e_{RC}C - e_{RC}h_{RC}CR^* + e_{RC}h_{RC}C^*R^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right) \\
& \left[\frac{e_C h_{RC}C^*\left(R - R^*\right) + e_{RC}\left[\left(C^* - C\right) + h_{RC}R^*\left(C^* - C\right)\right]}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right] \\
=& -\left(R - R^*\right)^2 + \left(R - R^*\right)\left[\frac{e_{RC}h_{RC}C^*\left(R - R^*\right) - e_{RC}\left(1 + h_{RC}R^*\right)\left(C - C^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]
\end{aligned}
$$

Likewise we have

$$
\begin{aligned}
\frac{dV_2(C)}{dt} =& \frac{dV_2}{dC}\frac{dC}{dt} \\
=& \left[1 - C^*\left(\frac{C^*}{C}\right)\frac{1}{C^*}\right]\left[rC(1 - C) + \frac{\alpha_{RC}RC}{1 + h_{RC}R + h_C C}\right] \\
=& \left(C - C^*\right)\left[r - rC + \frac{\alpha_{RC}R}{1 + h_{RC}R + h_C C}\right]
\end{aligned}
$$

If $\left(R^*, C^*\right)$ exists, then R^* and C^* must satisfy

$$
\begin{aligned}
0 =& \, rC^*\left(1 - C^*\right) + \frac{\alpha_{RC}R^*C^*}{1 + h_{RC}R^* + h_C C^*} \\
\Rightarrow 0 =& \, r\left(1 - C^*\right) + \frac{\alpha_{RC}R^*}{1 + h_{RC}R^* + h_C C^*} \\
\Leftrightarrow r =& \, rC^* - \frac{\alpha_{RC}R^*}{1 + h_{RC}R^* + h_C C^*}
\end{aligned}
$$

$$\frac{dV_2(C)}{dt} = \left(C - C^*\right)\left[rC^* - rC + \frac{\alpha_{RC}R}{1 + h_{RC}R + h_C C} - \frac{\alpha_{RC}R^*}{1 + h_{RC}R^* + h_C C^*}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)$$

$$\left[\frac{\alpha_{RC}R\left(1 + h_{RC}R^* + h_C C^*\right) - \alpha_{RC}R^*\left(1 + h_{RC}R + h_C C\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)\left[\frac{\alpha_{RC}R - \alpha_{RC}R^* + \alpha_{RC}h_C RC^* - \alpha_{RC}h_C CR^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)$$

$$\left[\frac{\alpha_{RC}R - \alpha_{RC}R^* + \alpha_{RC}h_C RC^* - \alpha_{RC}h_C CR^* + \alpha_{RC}h_C C^* R^* - \alpha_{RC}h_C C^* R^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)$$

$$\left[\frac{\left(\alpha_{RC}h_C RC^* - \alpha_{RC}h_C C^* R^* + \alpha_{RC}R - \alpha_{RC}R^*\right) + \left(-\alpha_{RC}h_C CR^* + \alpha_{RC}h_C C^* R^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)\left[\frac{-\alpha_{RC}h_C R^*\left(C - C^*\right) + \alpha_{RC}\left(h_C C^* + 1\right)\left(R - R^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= -r\left(C - C^*\right)^2 + \left(C - C^*\right)\left[\frac{-\alpha_{RC}h_C R^*\left(C - C^*\right) + \alpha_{RC}\left(h_C C^* + 1\right)\left(R - R^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

Thus,

$$\frac{\partial V}{\partial t} = -\left(R - R^*\right)^2 + \left(R - R^*\right)\left[\frac{e_{RC}h_{RC}C^*\left(R - R^*\right) - e_{RC}\left(1 + h_{RC}R^*\right)\left(C - C^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$- \beta r\left(C - C^*\right)^2 + \beta\left(C - C^*\right)\left[\frac{-\alpha_{RC}h_C R^*\left(C - C^*\right) + \alpha_{RC}\left(h_C C^* + 1\right)\left(R - R^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$= \left(R - R^*\right)^2\left[-1 + \frac{e_{RC}h_{RC}C^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$+ \beta\left(C - C^*\right)^2\left[-r - \frac{\alpha_{RC}h_C R^*}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\right]$$

$$+ \frac{\beta\alpha_{RC}\left(h_C C^* + 1\right) - e_{RC}\left(1 + h_{RC}C^*\right)}{\left(1 + h_{RC}R^* + h_C C^*\right)\left(1 + h_{RC}R + h_C C\right)}\left(R - R^*\right)\left(C - C^*\right)$$

To get the coefficient of the $\left(R - R^*\right)\left(C - C^*\right)$ term to equal zero, we must have

$$0 = \beta\alpha_{RC}\left(h_C C^* + 1\right) - e_{RC}\left(1 + h_{RC}R^*\right)$$

$$\Rightarrow \beta = \frac{e_{RC}\left(1 + h_{RC}R^*\right)}{\alpha_{RC}\left(1 + h_C C^*\right)}$$

This gives

$$\frac{\partial V}{\partial t} = \left[-1 + \frac{e_{RC}h_{RC}C^*}{(1 + h_{RC}R^* + h_C C^*)(1 + h_{RC}R + h_C C)}\right](R - R^*)^2$$
$$- \frac{e_{RC}(1 + h_{RC})}{\alpha_{RC}(1 + h_C C^*)}\left[r + \frac{\alpha_{RC}h_C R^*}{(1 + h_{RC}R^* + h_C C^*)(1 + h_{RC}R + h_C C)}\right](C - C^*)^2$$

The coefficient of the $(C - C^*)^2$ term is always negative. So if the coefficient of the $(R - R^*)^2$ term is also negative, then we will have $\frac{\partial V}{\partial t} < 0$. Thus, we want

$$-1 + \frac{e_{RC}h_{RC}C^*}{(1 + h_{RC}R^* + h_C C^*)(1 + h_{RC}R + h_C C)}$$
$$= -1 + h_{RC}\frac{e_{RC}C^*}{(1 + h_{RC}R^* + h_C C^*)(1 + h_{RC}R + h_C C)} < 0$$

But R^* and C^* satisfy

$$1 - R^* - \frac{e_{RC}C^*}{1 + h_{RC}R^* + h_C C^*} = 0$$
$$\Rightarrow 1 - R^* = \frac{e_{RC}C^*}{1 + h_{RC}R^* + h_C C^*}$$

But,

$$-1 + \frac{e_{RC}h_{RC}C^*}{(1 + h_{RC}R^* + h_C C^*)(1 + h_{RC}R + h_C C)} < -1 + h_{RC}\frac{e_{RC}C^*}{(1 + h_{RC}R^* + h_C C^*)}$$
$$= -1 + h_{RC}(1 - R^*)$$

Thus, if

$$h_{RC}(1 - R^*) < 1 \Leftrightarrow h_{RC} < \frac{1}{1 - R^*} \Leftrightarrow R^* > 1 - \frac{1}{h_{RC}} \tag{3.35}$$

then (R^*, C^*) will be globally asymptotically stable when it exists. $\square$

3.3.5   Simulations

In case (1)(a) when there are three interior equilibria, our system undergoes a subcritial Hopf bifurcation near the equilibrium with minimal R^*, as seen in figure 3.7.
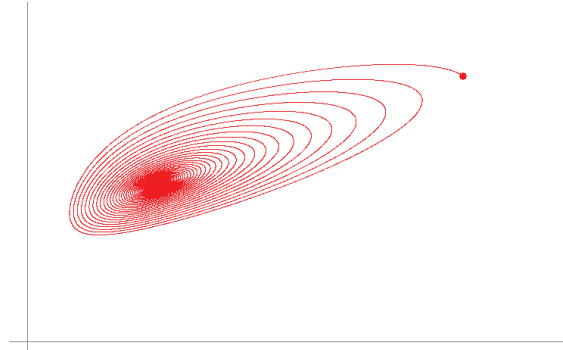
(a) $h_{RC} = 1001$, $h_C = 0.01$, $e_{RC} = 0.1935266666$, $r = 0.033333$, $\alpha_{RC} = 852.685166666$, initial conditions: $(0.0012, 12.5)$, forward time
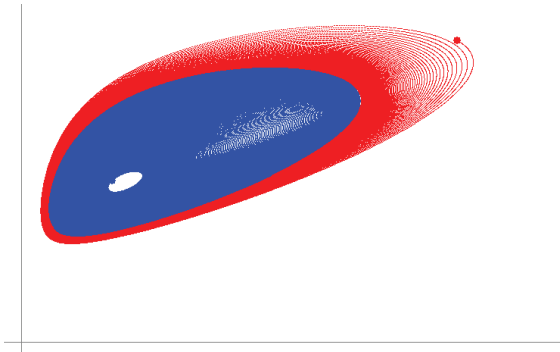
(b) $h_{RC} = 1001$, $h_C = 0.0001$, $e_{RC} = 0.1935266666$, $r = 0.033333$, $\alpha_{RC} = 852.685166666$, initial conditions: $(0.00025, 6.7)$ and $(0.0012, 12.5)$, backward time
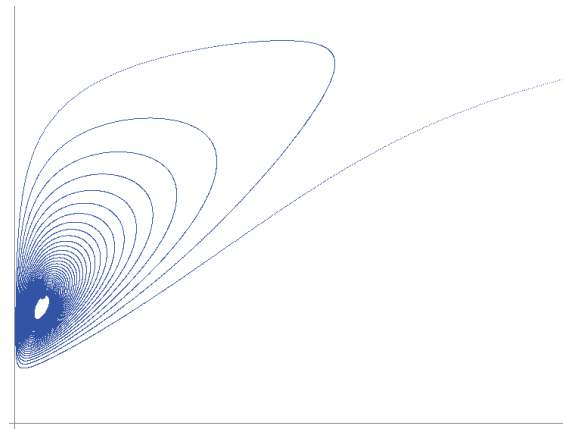
(c) $h_{RC} = 1001$, $h_C = -0.01$, $e_{RC} = 0.1935266666$, $r = 0.033333$, $\alpha_{RC} = 852.685166666$, initial conditions: $(0.00025, 6.7)$, forward time

Figure 3.7: *Subcritical Hopf bifurcation as h_C changes.*

Chapter 4

Analysis of the Full Model without Harvesting

4.1 Dissipativity

We now consider the full non-dimensionalized system:

$$
\begin{aligned}
\frac{dR}{dt} &= R\left(1 - R\right) - \frac{e_{RC}CR}{1 + h_{RC}R + h_{PCP}P + h_C C} - \frac{e_{RP}PR}{1 + h_{RP}R + h_{CP}C + P} \\
\frac{dC}{dt} &= rC\left(1 - C\right) + \frac{\alpha_{RC}RC}{1 + h_{RC}R + h_{CPP}P + h_C C} - \frac{e_{CP}PC}{1 + h_{RP}R + h_{CP}C + P} \\
\frac{dP}{dt} &= \frac{\alpha_{RP}RP}{1 + h_{RP}R + h_{PC}C + P} + \frac{\alpha_{CP}CP}{1 + h_{RP}R + h_{CP}C + P} - m_P P
\end{aligned}
\tag{4.1}
$$

In order to establish dissipativity of the full system, we need the following lemma.

Lemma 4.1. *Consider the equation*

$$
\frac{dx}{dt} = \frac{ax}{1 + bx} - cx.
\tag{4.2}
$$

(i) *If $a < c$ then $x_0 = 0$ is the unique non-negative equilibrium point and it is stable.*

(ii) *If $a > c$ then $x_0 = 0$ is an unstable equilibrium and $x_1 = \frac{a-c}{bc}$ is stable.*

Proof. We first determine the equilibria of this equation.

$$\frac{ax}{1+bx} - cx = 0$$

$$x\left(\frac{a}{1+bx} - c\right) = 0$$

So,

$$x = 0 \;\; \text{or} \;\; \frac{a}{1+bx} - c = 0$$

$$\frac{a}{1+bx} = c$$

$$1 + bx = \frac{a}{c}$$

$$x = \frac{a-c}{bc}$$

So the equilibria are $x_0 = 0$ and $x_1 = \frac{a-c}{bc}$ and if $a < c$ then x_1 is negative so that x_0 is the only non-negative equilibrium.

We next determine the stability of each of the equilibria by linearizing about the equilibria. To this end, we have

$$f'(x) = \frac{(1+bx)(a) - ax(b)}{(1+bx)^2} - c$$

$$= \frac{a}{(1+bx)^2} - c$$

At $x = x_0$ we get

$$f'(0) = a - c$$

If $a < c$ then $f'(0) < 0$ so that $x_0 = 0$ is stable. At $x = x_1$ we get

$$
\begin{aligned}
f'\left(\frac{a-c}{bc}\right) &= \frac{a}{\left[1 + b\left(\frac{a-c}{bc}\right)\right]^2} - c \\
&= \frac{a}{\left(1 + \frac{a-c}{c}\right)^2} - c \\
&= \frac{a}{\frac{a^2}{c^2}} - c \\
&= \frac{c^2}{a} - c \\
&= c\left(\frac{c}{a} - 1\right)
\end{aligned}
$$

If $a > c$, which is the case when $x_1 > 0$, then $f'(x_1) < 0$ and $f'(x_0) > 0$ so that $x_1 = \frac{a-c}{bc}$ is stable and $x_0 = 0$ is unstable. $\qquad \square$

Theorem 4.2. *The system (4.1) is dissipative.*

Proof. From the first equation in the system we have

$$
\frac{dR}{dt} \le R(1 - R)
$$

so the resource equation is a lower solution to the logistic equation. Thus, $\forall \, \varepsilon > 0 \, \exists \, t_1 = t_1(R_0)$ such that $R < 1 + \varepsilon$ for $t \ge t_1$. In particular, there must be a t_1 such that $R(t) < 2 \, \forall \, t \ge t_1$.

From the second equation in the system we have

$$
\begin{aligned}
\frac{dC}{dt} &\le rC(1 - C) + \frac{\alpha_{RC} RC}{1 + h_{RC}R + h_{CPP}P + h_C C} \\
&\le rC(1 - C) + \frac{\alpha_{RC} RC}{1 + h_C C}
\end{aligned}
$$

Thus, for $t \ge t_1$, the consumer equation is a lower solution to equation (3.30). We have already established that $\exists \, t_C = t_C(C_0)$ such that $C < v_1 + \varepsilon$ for $t \ge t_C$. In particular, there must be a t_C such that $C(t) < 2v_1 \, \forall \, t \ge t_C$.

From the third equation in the system we have

$$\frac{dP}{dt} \le \frac{\alpha_{RP}RP}{1+P} + \frac{\alpha_{CP}CP}{1+P} - m_pP$$

If $t \ge t_C$ then the predator equation is a lower solution to the equation

$$\begin{aligned}\frac{dy}{dt} &= \frac{2\alpha_{RP}y}{1+y} + \frac{2\alpha_{CP}v_1y}{1+y} - m_Py \\ &= \frac{2\left(\alpha_{RP} + \alpha_{cp}v_1\right)y}{1+y} - m_Py\end{aligned}$$

which is equation (4.2) with $a = 2\left(\alpha_{RP} + \alpha_{cp}v_1\right)$, $b = 1$, $c = m_P$.

Lemma (4.1) tells us that if $2(\alpha_{RP} + \alpha_{CP}v_1) < m_P$ then $x_0 = 0$ is stable. So $\forall\, \varepsilon > 0\, \exists\, t_4 = t_4(P_0)$ such that $P < \varepsilon$ for $t \ge t_4$. And if $2(\alpha_{RP} + \alpha_{CP}v_1) > m_P$ then $x_0 = 0$ is unstable, but $x_1 = \frac{2(\alpha_{RP}+\alpha_{CP}v_1)-m_P}{m_P}$ is stable, so $\forall\, \varepsilon > 0\, \exists\, t_5 = t_5(P_0)$ such that $P < x_1 + \varepsilon$ for $t \ge t_5$. In either case, $\exists\, t_P(P_0) = \max\left(t_4, t_5\right)$ such that $P(t) < x_1 + \varepsilon$ for $t \ge t_P$.

Thus, $\exists\, t_* > 0$ such that

$$R(t) < 1 + \varepsilon$$
$$C(t) < v_1 + \varepsilon$$
$$P(t) < x_1 + \varepsilon$$

for $t \ge t_*$. Thus, system (4.1) is dissipative. $\qquad\square$

4.2 Bounds on Boundary Equilibria

4.2.1 Bounds in the (R, P)-Plane and (C, P)-Plane

In the $R-P$ subsystem (3.6), the logistic equation is a supersolution to the R equation. So, we have that

$$R^* \leq K_R. \tag{4.3}$$

In the $C - P$ subsystem (3.1), the logistic equation is a supersolution to the C equation. So, we have that

$$C^* \leq K_C. \tag{4.4}$$

In order to get the upper bound on P^* in the (R, P)-plane, we first note that from Cantrell and Cosner [14], we have

$$\begin{aligned} P^* &= \frac{\alpha_{RP} e_{RP} R^* - m_P \left(1 + e_{RP} h_{RP} R^*\right)}{m_P e_P h_P} \\ &= \frac{R^* e_{RP}(\alpha_{RP} - m_P h_{RP}) - m_P}{m_P e_P h_P} \end{aligned}$$

and in the (C, P)-plane, we have

$$\begin{aligned} P^* &= \frac{\alpha_{CP} e_{CP} C^* - m_P \left(1 + e_{CP} h_{CP} R^*\right)}{m_P e_P h_P} \\ &= \frac{C^* e_{CP}(\alpha_{CP} - m_P h_{CP}) - m_P}{m_P e_P h_P}. \end{aligned}$$

In the (R, P)-plane, this gives us

$$P^* = \frac{R^* \left(\alpha_{RP} e_{RP} K_R - e_{RP} h_{RP} K_R m_P\right) - m_P}{e_P h_P m_P}.$$

In dimensionalized terms this becomes

$$
\begin{aligned}
P^* &= \frac{\frac{1}{K_R}R^*\left(\alpha_{RP}e_{RP}K_R - e_{RP}h_{RP}K_R m_P\right) - m_P}{e_P h_P m_P} \\
&= \frac{R^*\left(\alpha_{RP}e_{RP} - e_{RP}h_{RP}m_P\right) - m_P}{e_P h_P m_P}
\end{aligned}
$$

Thus, using inequality (4.3), we have that

$$
P^* < \frac{\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{e_P h_P m_P} \tag{4.5}
$$

which implies

$$
P^* < \frac{K_R \alpha_{RP} e_{RP}}{e_P h_P m_P}. \tag{4.6}
$$

Similarly, in the (C, P)-plane, we get

$$
P^* < \frac{\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{e_P h_P m_P} \tag{4.7}
$$

which implies

$$
P^* < \frac{K_C \alpha_{CP} e_{CP}}{e_P h_P m_P}. \tag{4.8}
$$

The qualitative behavior of inequalities (4.5) and (4.6) is the same if

$$
m_P < \frac{\alpha_{RP}}{h_{RP}}. \tag{4.9}
$$

Likewise, the qualitative behavior of inequalities (4.7) and (4.8) is the same if

$$
m_P < \frac{\alpha_{CP}}{h_{CP}}. \tag{4.10}
$$

Thus, anytime we use the upper bound on P^* in the (R, P)-plane or (C, P)-plane, we will assume inequalities (4.9) or (4.10) hold.

Biological Remark: The assumption that inequalities (4.9) and (4.10) hold is not

unreasonable to assume biologically. Inequality (4.9) says that the efficiency with which the predators gain from consuming the resource compared to the time they spend handling encountered resource is greater than the predators' natural mortality rate. In fact, this is a necessary condition for the predators' growth rate to be positive. To see this, note that

$$
\begin{aligned}
0 \leq \frac{dP}{dt} &= \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_P h_P P} - m_P P \\
&= \frac{\alpha_{RP}}{h_{RP}} P \left(\frac{e_{RP} R}{e_{RP} R + \frac{1}{h_{RP}}(1 + e_P h_P P)} \right) - m_P P \\
&\leq \frac{\alpha_{RP}}{h_{RP}} P - m_P P \\
&= \left(\frac{\alpha_{RP}}{h_{RP}} - m_P \right) P
\end{aligned}
$$

Furthermore, the interior equilibrium $\left(R^*, P^*\right)$ exists in the (R, P)-plane if and only if inequality (3.7) is satisfied. But inequality (3.7) implies inequality (4.9). So having the interior equilibrium $\left(R^*, P^*\right)$ in the (R, P)-plane is sufficient for having inequality (4.9) hold. Similarly, having inequality (3.3) is sufficient for having inequality (4.10) hold.

To get lower bounds on R^* and C^* we first note that in the (R, P)-plane, at equilibrium, we have

$$
\begin{aligned}
r_R \left(1 - \frac{R^*}{K_R} \right) &= \frac{e_{RP} P^*}{1 + e_{RP} h_{RP} R^* + e_P h_P P^*} \\
&\leq \frac{e_{RP} P^*}{1 + e_P h_P P^*}
\end{aligned}
$$

If we solve for R^*, we get

$$
R^* \geq K_R \left(1 - \frac{e_{RP} P^*}{r_R \left(1 + e_P h_P P^*\right)} \right) \tag{4.11}
$$

If we use inequality (4.6) in inequality (4.11) then we get

$$R^* \geq K_R \left(1 - \frac{\frac{\alpha_{RP} e_{RP}^2 K_R}{e_P h_P m_P}}{r_R \left(1 + \frac{\alpha_{RP} e_{RP} K_R}{m_P} \right)} \right) \tag{4.12}$$

Now, we will assume $2e_{RP} \leq r_R e_P h_P$. We will see what the reasons for this assumption are momentarily. But first, let us note that

$$2e_{RP} \leq r_R e_P h_P \Rightarrow 2e_{RP}(\alpha_{RP} e_{RP} K_R) < r_R e_P h_P(\alpha_{RP} e_{RP} K_R)$$

$$\Rightarrow 2\alpha_{RP} e_{RP}^2 K_R \leq r_R e_P h_P \alpha_{RP} e_{RP} K_R + r_R e_P h_P m_P$$

$$\Rightarrow \frac{\alpha_{RP} e_{RP}^2 K_R}{r_R(e_P h_P m_P + e_P h_P \alpha_{RP} e_{RP} K_R)} \leq \frac{1}{2}$$

$$\Leftrightarrow \frac{\frac{\alpha_{RP} e_{RP}^2 K_R}{e_P h_P m_P}}{r_R \left(1 + \frac{\alpha_{RP} e_{RP} K_R}{m_P} \right)} \leq \frac{1}{2}$$

$$\Rightarrow R^* \geq \frac{K_R}{2}$$

Remark: The above calculation shows that $2e_{RP} < r_R e_P h_P$ is a sufficient condition for having $R^* \geq \frac{K_R}{2}$. One reason for making this assumption is that working with a lower bound of $\frac{K_R}{2}$ is more analytically tractable than working with $\frac{\frac{\alpha_{RP} e_{RP}^2 K_R}{e_P h_P m_P}}{r_R \left(1 + \frac{\alpha_{RP} e_{RP} K_R}{m_P} \right)}$. The other reason is bioeconomic in nature.

Biological Remarks:

1. In the case where we have a single species growing logistically subject to constant effort harvesting, if the harvesters are harvesting with the optimal level of effort to attain the maximum sustainable yield, the equilibrium population density is $\frac{K}{2}$. As noted in Clark 2005, any level of effort greater than the optimal level will cause the stock resource to be driven asymptotically to extinction, which produces no yield. Thus, it is reasonable to assume that any harvesters who want to avoid resource extinction will harvest with an effort less than or equal to the optimal effort, which means the resource population density will be at

least $\frac{K}{2}$.

2. The condition $2e_{RP} \leq r_R e_P h_P$ put a limit on the rate at which the predators can attack the resource relative to the resource's intrinsic growth rate and the amount of intraspecific interference among the predators. The larger r_R is or the more intraspecific interference among the predators there is, the more the predators can attack the resource. The idea of having a limit on the rate at which the predators attack the resource is already present in this model. Note that in the (R, P)-plane, if the resource population is going to grow, we must have

$$0 \leq \frac{dR}{dt} = r_R R \left[1 - \frac{R}{K_R} - \frac{e_{RP}}{r_R e_P h_P} \left(\frac{P}{\frac{1}{e_P h_P} + \frac{e_{RP} h_{RP}}{e_P h_P} R + P} \right) \right]$$
$$\leq r_R R \left(1 - \frac{e_{RP}}{r_R e_P h_P} \right)$$

So, it is necessary to have $e_{RP} < r_R e_P h_P$ if the resource population is to grow. In other words, it is already a necessary condition to have a limit on the rate at which the predators can attack the resource in this model.

So, in the (R, P)-plane, we have

$$R^* \geq \frac{K_R}{2}. \tag{4.13}$$

Similarly, if we require $2e_{CP} \leq r_C e_P h_P$ then in the (C, P)-plane, we have

$$C^* \geq \frac{K_C}{2}. \tag{4.14}$$

To get the lower bound on P in the (R, P)-plane, note that we have

$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P} - m_P P.$$

By inequalities (4.13) and (4.3), we have $\frac{K_R}{2} < R^* < K_R$. So, we have that

$$\frac{dP}{dt} \geq \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R P}{1 + e_{RP}h_{RP}K_R + e_P h_P P} - m_P P.$$

Let $\tilde{P}$ be a solution to

$$\frac{d\tilde{P}}{dt} \geq \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R \tilde{P}}{1 + e_{RP}h_{RP}K_R + e_P h_P \tilde{P}} - m_P \tilde{P}.$$

Then $\tilde{P}$ is a subsolution to the predator equation and at equilibrium,

$$\tilde{P} = \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P \left(1 + e_{RP}h_{RP}K_R\right)}{e_P h_P m_P}.$$

Thus,

$$P^* \geq \max\left\{0, \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P \left(1 + e_{RP}h_{RP}K_R\right)}{e_P h_P m_P}\right\}. \tag{4.15}$$

In the (C, P)-plane,

$$P^* \geq \max\left\{0, \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P \left(1 + e_{CP}h_{CP}K_C\right)}{e_P h_P m_P}\right\}. \tag{4.16}$$

4.2.2 Bounds in the (R, C)-Plane

In the (R, C)-plane, the logistic equation is a supersolution to the resource equation and a subsolution to the consumer equation. Thus we know that $R^* \leq K_R$ and $C^* \geq K_C$.

For R^*, we have three possibilities when $e_{RC} > r_R e_C h_C$ and one possibility when $e_{RC} < r_R e_C h_C$. When $e_{RC} > r_R e_C h_C$, we could have $0 \leq R^* \leq K_R$, $0 \leq R^* \leq \frac{1}{2}K_R$, or $\frac{1}{2}K_R \leq R^* \leq K_R$. When $e_{RC} > r_R e_C h_C$, we have $K_R\left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) \leq R^* \leq K_R$. In case (1)(a) when there is one interior equilibrium, we could either have $0 \leq R \leq \frac{1}{2}K_R$ or $\frac{1}{2} \leq R^* \leq K_R$. When there are three interior equilibria, we have two equilibria with $0 \leq R^* \leq \frac{1}{2}K_R$ and one equilibrium with $\frac{1}{2}K_R \leq R^* \leq K_R$. In case (1)(b) when there

are two interior equilibria, we have one equilibrium with $0 \leq R^* \leq K_R$ and one with $\frac{1}{2}K_R \leq R^* \leq K_R$. In case (2) there is one interior equilibrium with $0 \leq R^* \leq K_R$. In case (3) there is one interior equilibrium with $K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) \leq R^* \leq K_R$.

The consumer equation in the (R, C)-plane is

$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C}.$$

For the upper bound on C^*, we can either find a supersolution to this equation or we can use the consumer isocline's horizontal asymptote. The consumer isocline's horizontal asymptote, in dimensionalized terms, is $C = K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}}$. The values of the parameters determine which upper bound is sharper.

If we use the resource isocline's horizontal asymptote to bound C^*, then

$$C^* \leq K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}}. \tag{4.17}$$

If $0 < R^* \leq K_R$, we have that

$$\frac{dC}{dt} \leq r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R C}{1 + e_{RC} h_{RC} R + e_C h_C C}$$
$$\leq r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R C}{1 + e_C h_C C}$$

Let $\tilde{C}$ be a solution to

$$\frac{d\tilde{C}}{dt} = r_C \tilde{C} \left(1 - \frac{\tilde{C}}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R \tilde{C}}{1 + e_C h_C K_C}.$$

Then $\tilde{C}$ is a supersolution to the consumer equation and at equilibrium,

$$\tilde{C} = K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C (1 + e_C h_C K_C)}.$$

So,

$$C^* \leq K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C(1 + e_C h_C K_C)}. \tag{4.18}$$

Thus, if $\frac{e_{RC} K_R}{1 + e_C h_C K_C} < \frac{1}{h_{RC}} \Leftrightarrow e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$ then (4.18) gives us a sharper bound on C^*. But, if $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$ then (4.17) gives us a sharper bound on C^*.

If $0 < R^* \leq \frac{1}{2} K_R$ then $C^* \leq K_C + \frac{\frac{1}{2} K_C \alpha_{RC} e_{RC} K_R}{r_C(1 + e_C h_C K_C)}$ if $\frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$ and $C^* \leq K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}}$ if $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$.

If $\frac{1}{2} K_R < R^* < K_R$ then

$$\frac{dC}{dt} \leq r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R C}{1 + e_{RC} h_{RC} R + e_C h_C C}$$

$$\leq r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R C}{1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C C}$$

Let $\tilde{C}$ be a solution to

$$\frac{d\tilde{C}}{dt} = r_C \tilde{C} \left(1 - \frac{\tilde{C}}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R \tilde{C}}{1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C}.$$

Then $\tilde{C}$ is a supersolution to the consumer equation and at equilibrium,

$$\tilde{C} = K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C\right)}$$

So,

$$C^* \leq K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C\right)}. \tag{4.19}$$

Thus, if $\frac{e_{RC} K_R}{1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C} < \frac{1}{h_{RC}} \Leftrightarrow \frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$ then (4.19) gives us a sharper bound on C^*. But, if $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$ then (4.17) gives us a sharper bound on C^*.

If $K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) < R^* \leq K_R$ then

$$\frac{dC}{dt} \leq r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R C}{1 + e_{RC} h_{RC} R + e_C h_C K_C}$$

$$\leq \frac{\alpha_{RC} e_{RC} K_R C}{1 + e_{RC} h_{RC} K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C}$$

Let $\tilde{C}$ be a solution to

$$\frac{d\tilde{C}}{dt} = r_C \tilde{C} \left(1 - \frac{\tilde{C}}{K_C}\right) + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C}.$$

Then $\tilde{C}$ is a supersolution to the consumer equation and at equilibrium,

$$\tilde{C} = K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C \left[1 + e_{RC} h_{RC} K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C\right]}.$$

So,

$$\tilde{C} \leq K_C + \frac{K_C \alpha_{RC} e_{RC} K_R}{r_C \left[1 + e_{RC} h_{RC} K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C\right]}. \tag{4.20}$$

Thus, if $\frac{e_{RC} K_R}{1 + e_{RC} h_{RC} K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C} < \frac{1}{h_{RC}} \Leftrightarrow e_{RC}^2 h_{RC} K_R < r_R e_C h_C (1 + e_C h_C K_C)$ then (4.20) gives us a sharper bound on C^*. But, if $r_R e_C h_C (1 + e_C h_C K_C) < e_{RC}^2 h_{RC} K_R$ then (4.17) gives us a sharper bound on C^*. Note that $r_R e_C h_C (1 + e_C h_C K_C) < e_{RC}^2 h_{RC} K_R \Leftrightarrow 1 + e_C h_C K_C < e_{RC} h_{RC} K_R$.

4.2.3 Summary of Bounds on Boundary Equilibria

Combining inequalities (4.13) and (4.3), we have that in the (R, P)-plane

$$\frac{K_R}{2} < R^* < K_R \tag{4.21}$$

$$\max\left\{0, \frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P (1 + e_{RP} h_{RP} K_R)}{e_P h_P m_P}\right\} \leq P^* \leq \frac{K_R \alpha_{RP} e_{RP}}{e_P h_P m_P}. \tag{4.22}$$

If we combine inequalities (4.14) and (4.4), then in the (C, P)-plane we have

$$\frac{K_C}{2} < C^* < K_C \tag{4.23}$$

$$\max\left\{0, \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right)}{e_P h_P m_P}\right\} \leq P^* \leq \frac{K_C \alpha_{CP}e_{CP}}{e_P h_P m_P}. \tag{4.24}$$

And in the (R, C)-plane, we have either

$$0 \leq R^* \leq K_R \text{ and } K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}e_{RC}K_R}{r_C(1 + e_C h_C K_C)} \text{ if } e_{RC}h_{RC}K_R < 1 + e_C h_C K_C \tag{4.25}$$

$$0 \leq R^* \leq K_R \text{ and } K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}} \text{ if } 1 + e_C h_C K_C < e_{RC}h_{RC}K_R \tag{4.26}$$

or

$$\frac{1}{2}K_R \leq R^* \leq K_R \text{ and } K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}e_{RC}K_R}{r_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}$$

$$\text{if } \frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C \tag{4.27}$$

$$\frac{1}{2}K_R \leq R^* \leq K_R \text{ and } K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}}$$

$$\text{if } 1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R. \tag{4.28}$$

or

$$K_R\left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) < R^* \leq K_R \text{ and}$$

$$K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}e_{RC}K_R}{r_C\left[1 + e_{RC}h_{RC}K_R\left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C\right]}$$

$$\text{if } e_{RC}^2 h_{RC}K_R < r_R e_C h_C(1 + e_C h_C K_C) \tag{4.29}$$

$$\frac{1}{2}K_R \leq R^* \leq K_R \text{ and } K_C \leq C^* \leq K_C + \frac{K_C \alpha_{RC}}{r_C h_{RC}}$$

$$\text{if } r_R e_C h_C(1 + e_C h_C K_C) < e_{RC}^2 h_{RC}K_R \tag{4.30}$$

4.3 Invasibility & Exclusion when all Species Absent

$$J(0,0,0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & r & 0 \\ 0 & 0 & -m_P \end{bmatrix}$$

$(0,0,0)$ is a saddle where the (R,C)-plane is the unstable subspace and the P-axis is the stable subspace. Even though the predator is not able to invade, the system could still be permanent. Since the resource and consumer can invade, they can establish themselves in the (R,C)-plane which the predator might then be able to invade.

4.4 Invasibility & Exclusion When the Consumers and Predators are Absent

$$J(1,0,0) = \begin{bmatrix} -1 & -\frac{e_{RC}}{1+h_{RC}} & -\frac{e_{RP}}{1+h_{RP}} \\ 0 & r + \frac{\alpha_{RC}}{1+h_{RC}} & 0 \\ 0 & 0 & \frac{\alpha_{RP}}{1+h_{RP}} - m_P \end{bmatrix}$$

So $\lambda_1 = -1, \lambda_2 = \frac{r+rh_{RC}+\alpha_{RC}}{1+h_{RC}} > 0, \lambda_3 = \frac{\alpha_{RP}-m_P-h_{RP}m_P}{1+h_{RP}}$. Thus, $(1,0,0)$ is always a saddle which is stable along the R-axis and unstable along the C-axis. Thus, the consumer will always be able to invade this system. If the predator is also to be able to invade this system, we need $(1,0,0)$ to be unstable along the P-axis so that both of the missing species can invade. Thus, we need $\alpha_{RP} > m_P (1 + h_{RP})$. In dimensionalized terms, this becomes

$$\alpha_{RP} e_{RP} K_R > m_P (1 + e_{RP} h_{RP} K_R). \tag{4.31}$$

We could write this equivalently as $\alpha_{RP} > m_P \left(h_{RP} + \frac{1}{e_{RP} K_R} \right)$. Notice that (4.31)

is condition (3.7), which tells us the condition needed for the interior equilibrium $\left(R^*, P^*\right)$ to exist in the $R-P$ subsystem. Thus, a necessary condition for the predator to be able to invade in this case is $\alpha_{RP} > m_P h_{RP}$, or equivalently, $\frac{\alpha_{RP}}{h_{RP}} > m_P$. This says that the rate at which the resource is converted into predators compared to the time predators spend handling the resource must be greater than the mortality rate of the predators. Thus, in order for both the consumer and predator to invade the system when both are absent and the basal resource is at equilibrium, the predator must gain sufficiently from consumed basal resource. Otherwise, the consumer will exclude the predator from being able to invade the system. But even if the consumer excludes the predator from the system, the consumer's ability to invade means the system could still be permanent. After the consumer establishes itself in the $R - C$ subsystem, the predator could then invade that system.

4.5 Invasibility & Exclusion When the Resource and Predators are Absent

$$J(0,1,0) = \begin{bmatrix} 1 - \frac{e_{RC}}{1+h_C} & 0 & 0 \\ \frac{\alpha_{RC}}{1+h_C} & -r & -\frac{e_{CP}}{1+h_{CP}} \\ 0 & 0 & \frac{\alpha_{CP}}{1+h_{CP}} - m_P \end{bmatrix}$$

So $\lambda_1 = 1 - \frac{e_{RC}}{1+h_C}, \lambda_2 = -r, \lambda_3 = \frac{\alpha_{CP}-m_P-h_{CP}m_P}{1+h_{CP}}$. Thus, in order for both the basal resource and the the top predator to be able to invade the system, we must have $\lambda_1 > 0$ and $\lambda_3 > 0$, or $e_{RC} < h_C + 1$ and $\alpha_{CP} > m_P (1 + h_{CP})$. The first of these conditions is inequality (3.33) which was the condition necessary for the $R - C$ subsystem to be permanent. In dimensionalized parameters, these conditions become

$$e_{RC} < \frac{r_R}{K_C} \left(1 + e_C h_C K_C\right) \tag{4.32}$$

and

$$\alpha_{CP} e_{CP} K_C > m_P \left(1 + e_{CP} h_{CP} K_C\right). \tag{4.33}$$

We can rewrite condition (4.33) equivalently as $\alpha_{CP} > m_P \left(h_{CP} + \frac{1}{e_{CP} K_C}\right)$. We recognize (4.33) as being inequality (3.3), which was the necessary condition for the equilibrium $\left(C^*, P^*\right)$ to exist in the $C - P$ plane. This gives us the necessary condition $\alpha_{CP} > m_P h_{CP}$, or equivalently $\frac{\alpha_{CP}}{h_{CP}} > m_P$, for the predator to be able to invade. This says that the rate at which the consumers are converted into predators per unit of time must be greater than the mortality rate of the predators. Thus, in order for both the basal resource and top predator to invade the system when both are absent and the consumer is at equilibrium, the consumer cannot encounter the basal resource too frequently and the predator must gain sufficiently from consumed consumers. If the consumers encounter the basal resource too often then the basal resource will be excluded from the system, and if the predator does not gain sufficiently from consuming the consumer then it will be excluded from the system.

4.6 Invasibility & Exclusion When the Resource is Absent

Assume $\alpha_{CP} e_{CP} K_C > \left(e_{CP} h_{CP} K_C + 1\right) m_P$. Then $\left(C^*, P^*\right)$ exists in the (C, P)-plane and the consumer-predator subsystem is permanent. Assume further that $e_{CP} h_{CP} K_C \left(1 - C^*\right) < 1$ so that $\left(C^*, P^*\right)$ is globally asymptotically stable. If we linearize the R equation about the equilibrium $\left(0, C^*, P^*\right)$, we get

$$\frac{dR}{dt} = \left(1 - \frac{e_{RC} C^*}{1 + h_{PCP} P^* + h_C C^*} - \frac{e_{RP} P^*}{1 + h_{CP} C^* + P^*}\right) R. \tag{4.34}$$

In order for the basal resource to invade this system, we need $\frac{dR}{dt} > 0$, which gives us (in dimensionalized terms)

$$r_R > \frac{e_{RC}C^*}{1 + e_{CP}h_{PC}P^* + e_C h_C C^*} + \frac{e_{RP}P^*}{1 + e_{CP}h_{CP}C^* + e_P h_P P^*}. \qquad (4.35)$$

If we have that

$$r_R < \frac{e_{RC}C^*}{1 + e_{CP}h_{PC}P^* + e_C h_C C^*} + \frac{e_{RP}P^*}{1 + e_{CP}h_{CP}C^* + e_P h_P P^*} \qquad (4.36)$$

then the resource will be excluded from the system. If we use the bounds on C^* and P^* given by inequalities (4.23) and (4.24), then we get two possibilities, depending on whether $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) > 0$ or $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$. If $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) > 0$ then invasibility condition (4.35) becomes

$$r_R > \frac{e_{RC}K_C}{1 + e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{e_P h_P m_P}\right] + \frac{1}{2}e_C h_C K_C}$$

$$+ \frac{\frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_P h_P m_P}}{1 + \frac{1}{2}e_{CP}h_{CP}K_C + \left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{m_P}\right]}$$

We can simplify the denominator of the second fraction to get

$$1 + \frac{1}{2}e_{CP}h_{CP}K_C + \left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right)}{m_P}\right]$$

$$= 1 + \frac{1}{2}e_{CP}h_{CP}K_C + \frac{\alpha_{CP}e_{CP}K_C}{2m_P} - 1 - e_{CP}h_{CP}K_C$$

$$= \frac{\alpha_{CP}e_{CP}K_C}{2m_P} - \frac{1}{2}e_{CP}h_{CP}K_C$$

$$= \frac{1}{2}e_{CP}K_C\left(\frac{\alpha_{CP}}{m_P} - h_{CP}\right)$$

Thus, the second fraction becomes

$$\frac{\frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_Ph_Pm_P}}{1+\frac{1}{2}e_{CP}h_{CP}K_C+\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C-m_P(1+e_{CP}h_{CP}K_C)}{m_P}\right]} = \frac{\frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_Ph_Pm_P}}{\frac{1}{2}e_{CP}K_C\left(\frac{\alpha_{CP}}{m_P}-h_{CP}\right)}$$

$$= \frac{2e_{RP}\alpha_{CP}}{e_Ph_P\left(\alpha_{CP}-h_{CP}m_P\right)}$$

So, if $\frac{1}{2}\alpha_{CP}e_{CP}K_C-m_P\left(1+e_{CP}h_{CP}K_C\right)>0$ then invasibility condition (4.35) becomes

$$r_R > \frac{e_{RC}K_C}{1+e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C-m_P(1+e_{CP}h_{CP}K_C)}{e_Ph_Pm_P}\right]+\frac{1}{2}e_Ch_CK_C}+\frac{2e_{RP}\alpha_{CP}}{e_Ph_P\left(\alpha_{CP}-h_{CP}m_P\right)} \tag{4.37}$$

and exclusion condition (4.36) becomes

$$r_R < \frac{\frac{1}{2}e_{RC}K_C}{1+\frac{e_{CP}^2h_{PC}K_C\alpha_{CP}}{e_Ph_Pm_P}+e_Ch_CK_C}+\frac{e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C-m_P\left(1+e_{CP}h_{CP}K_C\right)\right]}{e_Ph_Pm_P\left(1+e_{CP}h_{CP}K_C\right)+e_Ph_PK_C\alpha_{CP}e_{CP}} \tag{4.38}$$

If $\frac{1}{2}\alpha_{CP}e_{CP}K_C-m_P\left(1+e_{CP}h_{CP}K_C\right)<0$ then invasibility condition (4.35) becomes

$$r_R > \frac{e_{RC}K_C}{1+\frac{1}{2}e_Ch_CK_C}+\frac{\frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_Ph_Pm_P}}{1+\frac{1}{2}e_{CP}h_{CP}K_C} \tag{4.39}$$

and exclusion condition (4.36) becomes

$$r_R < \frac{\frac{1}{2}e_{RC}K_C}{1+\frac{e_{CP}^2h_{PC}K_C\alpha_{CP}}{e_Ph_Pm_P}+e_Ch_CK_C} \tag{4.40}$$

Note that whether the basal resource is able to invade or is excluded from the system depends in part on parameters which are independent of resource itself.

Before stating the following theorem, we introduce some terminology.

Definition 4.1. *1. We say that increasing $e_C h_C$ makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ reduces the minimum value of r_R necessary for the resource to invade. We say that increasing $e_C h_C$ makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ increases the minimum value of r_R necessary for the resource to invade.*

2. We say that increasing $e_C h_C$ makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ increases the maximum value of r_R, below which the resource will be excluded. We say that increasing $e_C h_C$ makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ decreases the maximum value of r_R, below which the resource is excluded.

Theorem 4.3. *Increasing $e_C h_C$*

1. makes it easier for the resource to invade.

2. makes it harder for the resource to be excluded.

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) > 0$, the second fraction on the right hand side of invasibility condition (4.37) does not depend on e_C or h_C so increasing these parameter values does not change the resource's ability to invade. But the first fraction is of the form

$$f(e_C h_C) = \frac{A}{B + Ce_C h_C}$$

where

$$A = e_{RC}K_C$$

$$B = 1 + e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right)}{e_Ph_Pm_P}\right]$$

$$C = \frac{1}{2}K_C$$

We have that

$$f'(e_Ch_C) = -\frac{AC}{\left(B + Ce_Ch_C\right)^2} < 0$$

since $A, C > 0$. Thus, increasing e_Ch_C in this case makes it easier for the the resource to invade the system.

The second fraction on the right hand side of exclusion condition (4.38) does not depend on e_C or h_C so increasing these parameter values does not change whether or not the resource will be excluded from the system. But the first fraction is of the form

$$f(e_Ch_C) = \frac{A}{B + Ce_Ch_C}$$

where

$$A = \frac{1}{2}e_{RC}$$

$$B = 1 + \frac{e_{CP}^2h_{PC}K_C\alpha_{CP}}{e_Ph_Pm_P}$$

$$C = K_C$$

Since $A, C > 0$, we have that f is decreasing in e_Ch_C. So, increasing e_Ch_C makes it harder for the resource to be excluded from the system.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) < 0$, the second fraction on the right hand side of invasibility condition (4.39) does not depend on e_C or h_C so increasing the parameter values does not change the resource's ability to invade. But

the first fraction is of the form

$$f(e_C h_C) = \frac{A}{B + C e_C h_C}$$

where

$$A = e_{RC} K_C$$

$$B = 1$$

$$C = \frac{1}{2} K_C$$

Since $A, C > 0$, we have that f is decreasing in $e_C h_C$. So, increasing $e_C h_C$ makes it easier for the resource to invade the system.

The right hand side of exclusion condition (4.40) has the form

$$f(e_C h_C) = \frac{A}{B + C e_C h_C}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = 1 + \frac{e_{CP}^2 h_{PC} K_C \alpha_{CP}}{e_P h_P m_P}$$

$$C = K_C$$

Since $A, C > 0$, we have that f is decreasing in $e_C h_C$. Thus, increasing $e_C h_C$ makes it harder for the resource to be excluded from the system. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.2.   *1. We say that increasing K_C makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is*

a decreasing function of K_C; i.e., if increasing K_C reduces the minimum value of r_R necessary for the resource to invade. We say that increasing K_C makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of K_C; i.e., if increasing K_C increases the minimum value of r_R necessary for the resource to invade.

2. *We say that increasing K_C makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of K_C; i.e., if increasing K_C increases the maximum value of r_R, below which the resource will be excluded. We say that increasing K_C makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of K_C; i.e., if increasing K_C decreases the maximum value of r_R, below which the resource is excluded.*

Theorem 4.4. *Increasing K_C*

1. *makes it easier for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{CP}h_{PC} > e_P h_P$.*

2. *makes it harder for the resource to invade if*

   (a) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{CP}h_{PC} < e_P h_P$.*

   (b) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

3. *makes it easier for the resource to be excluded.*

Proof. We are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, provided that

$$
K_C \begin{cases} > \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}} & \text{if } \frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP} > 0 \\ < \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}} & \text{if } \frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP} < 0 \end{cases}.
$$

Note that if $\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP} < 0$ and $K_C < \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}$ then we get that $K_C < 0$, which we cannot have. So this case is not possible. So, we will be in this case if $\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP} > 0$ and $K_C > \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}$.

The second fraction on the right hand side of invasibility condition (4.37) is independent of K_C. The first fraction is of the form

$$f(K_C) = \frac{AK_C}{B + CK_C}$$

where

$$A = e_{RC}$$
$$B = 1 - \frac{e_{CP}h_{PC}}{e_P h_P}$$
$$C = e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}{e_P h_P m_P}\right] + \frac{1}{2}e_C h_C K_C$$

Since we are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) > 0$ and $K_C\left(\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}\right) = \frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P e_{CP}h_{CP}K_C > \frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)$, we have that $C > 0$. But, B could be positive or negative. We have that

$$f'(K_C) = \frac{AB}{(B + CK_C)^2} \begin{cases} > 0 \text{ if } B > 0 \\ \\ < 0 \text{ if } B < 0 \end{cases}.$$

So, $f'(K_C) > 0$ if $e_{CP}h_{PC} < e_P h_P$ and $f'(K_C) < 0$ if $e_{CP}h_{CP} > e_P h_P$.

Thus, increasing K_C causes the right hand side of invasibility condition (4.37) to increase when $e_{CP}h_{PC} < e_P h_P$. In this case, invasion is harder. But, increasing K_C causes the right hand side of invasibility condition (4.37) to decrease when $e_{CP}h_{PC} > e_P h_P$. In this case, invasion is easier.

The first fraction on the right hand side of exclusion condition (4.38) is of the

form

$$f(K_C) = \frac{AK_C}{B + CK_C}$$

where

$$A = \frac{1}{2}e_{RC}$$

$$B = 1$$

$$C = \frac{e_{CP}^2 h_{PC}\alpha_{CP}}{e_P h_P m_P} + e_C h_C$$

We have that

$$f'(K_C) = \frac{AB}{(B + CK_C)^2} > 0.$$

So, increasing K_C causes the first fraction on the right hand side of exclusion condition (4.38) to increase.

The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$g(K_C) = \frac{-D + EK_C}{F + GK_C}$$

where

$$D = e_{RP}m_P$$

$$E = e_{RP}\left(\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}\right)$$

$$F = e_P h_P m_P$$

$$G = e_P h_P m_P e_{CP}h_{CP} + \alpha_{CP}e_{CP}e_P h_P$$

As noted above, $\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP} > 0$ in this case, so $E > 0$. We have that

$$g'(K_C) = \frac{EF + DG}{(F + GK_C)^2} > 0.$$

So, increasing K_C causes the second fraction on the right hand side of exclusion condition (4.38) to increase.

Thus, increasing K_C causes both the first and second fractions on the right hand side of exclusion condition (4.38) to increase. When we add these fractions together, we get that the right hand side of exclusion condition (4.38) is increasing. This makes exclusion easier.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$, the first fraction on the right hand side of invasibility condition (4.39) is of the form

$$f(K_C) = \frac{AK_C}{B + CK_C}$$

where

$$A = e_{RC}$$
$$B = 1$$
$$C = \frac{1}{2}e_C h_C$$

We have that $f'(K_C) > 0$. So, increasing K_C increases the first fraction on the right hand side of invasibility condition (4.39).

The second fraction on the right hand side of invasibility condition (4.39) is of the form

$$g(K_C) = \frac{DK_C}{E + FK_C}$$

where

$$D = \frac{e_{RP}\alpha_{CP}e_{CP}}{e_P h_P m_P}$$

$$E = 1$$

$$F = \frac{1}{2}e_{CP}h_{CP}$$

We have that $g'(K_C) > 0$. So, increasing K_C increases the second fraction on the right hand side of invasibility condition (4.39).

Thus, increasing K_C causes both the first fraction and second fraction on the right hand side of invasibility condition (4.39) to increase. When we add these fractions together, we get that the right hand side of invasibility condition (4.39) is increasing. Therefore, increasing K_C makes invasibility harder.

The right hand side of exclusion condition (4.40) is of the form

$$f(K_C) = \frac{AK_C}{B + CK_C}$$

where

$$A = \frac{1}{2}e_{RC}$$

$$B = 1$$

$$C = \frac{e_{CP}^2 h_{PC}\alpha_{CP}}{e_P h_P m_P} + e_C h_C$$

We have that $f'(K_C) > 0$. So, increasing K_C increases the right hand side of exclusion condition (4.40). This makes exclusion easier. $\quad\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.3. *1. We say that increasing m_P makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a*

decreasing function of m_P; i.e., if increasing m_PC reduces the minimum value of r_R necessary for the resource to invade. We say that increasing m_P makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of m_P; i.e., if increasing m_P increases the minimum value of r_R necessary for the resource to invade.

2. *We say that increasing m_P makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of m_P; i.e., if increasing m_P increases the maximum value of r_R, below which the resource will be excluded. We say that increasing m_P makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of m_P; i.e., if increasing m_P decreases the maximum value of r_R, below which the resource is excluded.*

Theorem 4.5. *Increasing m_P*

1. *makes it easier for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

2. *makes it harder for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.*

3. *makes it easier for the resource to be excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} >> e_{RP}$.*

4. *makes it harder for the resource to be excluded if*

   (a) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} << e_{RP}$.*

   (b) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

Proof. We are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, provided that $m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$. The first fraction on the right hand side of invasibility

condition (4.37) is of the form

$$f(m_P) = \frac{Am_P}{B + Cm_P}$$

where

$$A = e_{RC}K_C$$
$$B = \frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{2e_P h_P}$$
$$C = 1 + \frac{1}{2}e_C h_C K_C - \frac{1 + e_{CP}h_{CP}K_C}{e_P h_P}$$

Here, C could be positive or negative. We have that

$$f'(m_P) = \frac{AB}{(B + Cm_P)^2} > 0$$

So, increasing m_P causes the first fraction on the right hand side of invasibility condition (4.37) to increase.

The second fraction on the right hand side of invasibility condition (4.37) is of the form

$$g(m_P) = \frac{E}{F - Gm_P}$$

where

$$E = 2e_{RP}\alpha_{CP}$$

$$F = e_P h_P \alpha_{CP}$$

$$G = e_P h_P h_{CP}$$

We have that

$$g'(m_P) = \frac{EG}{(F - Gm_P)^2} > 0$$

So, increasing m_P causes the second fraction on the right hand side of invasibility condition (4.37) to increase. Thus, increasing m_P causes both the first fraction and second fraction on the right hand side of invasibility condition (4.37) to increase. When we add these fractions together, we get that the entire right hand side increases as a result of increasing m_P, making invasion by the resource harder.

The first fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(m_P) = \frac{Am_P}{B + Cm_P}$$

where

$$A = \frac{1}{2}e_{RC}K_C$$
$$B = \frac{e_{CP}^2 h_{PC}K_C\alpha_{CP}}{e_P h_P}$$
$$C = 1 + e_C h_C K_C$$

We have that $f'(m_P) > 0$, so increasing m_P causes the first fraction on the right hand side of exclusion condition (4.38) to increase.

The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$g(m_P) = \frac{D - Em_P}{F + Gm_P}$$

where

$$D = \frac{1}{2}\alpha_{CP}e_{CP}e_{RP}K_C$$
$$E = e_{RP}(1 + e_{CP}h_{CP}K_C)$$
$$F = K_C\alpha_{CP}e_{CP}e_P h_P$$
$$G = e_P h_P(1 + e_{CP}h_{CP}K_C)$$

We have that

$$g'(m_P) = -\frac{EF + GD}{(F + Gm_P)^2} < 0$$

So, increasing m_P causes the second fraction on the right hand side of exclusion condition (4.38) to decrease.

Thus, increasing m_P causes the first fraction on the right hand side of exclusion condition (4.38) to increase while causing the second fraction to decrease. When we add these fractions together, we could have that the right hand side is increasing or decreasing as a result of increasing m_P. If $e_{RC} >> e_{RP}$, then the first fraction on the right hand side dominates the second fraction, so increasing m_P causes the right hand side to increase. This makes exclusion easier. But if $e_{RC} << e_{RP}$, then the second fraction on the right hand side dominates the first fraction, so increasing m_P causes the right hand side to decrease. This makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$, the first fraction on the right hand side of invasibility condition (4.39) does not depend on m_P. The second fraction has the form

$$f(m_P) = \frac{A}{m_P}$$

where

$$A = \frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_Ph_Pm_P\left(1 + \frac{1}{2}e_{CP}h_{CP}K_C\right)}$$

We have that

$$f'(m_P) = -\frac{A}{m_P^2} < 0$$

So, increasing m_P causes the right hand side of invasibility condition (4.39) to decrease, which makes invasion easier.

The right hand side of exclusion condition (4.40) is of the form

$$f(m_P) = \frac{Am_P}{B + Cm_P}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = \frac{e_{CP}^2 h_{PC} K_C \alpha_{CP}}{e_P h_P}$$

$$C = 1 + e_C h_C K_C$$

We have that $f'(m_P) > 0$, so increasing m_P causes the right hand side of exclusion condition (4.40) to decrease. This makes exclusion harder.

Before stating the following theorem, we introduce some terminology.

Definition 4.4. 1. *We say that increasing $e_P h_P$ makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of $e_P h_P$; i.e., if increasing $e_P h_P$ reduces the minimum value of r_R necessary for the resource to invade. We say that increasing $e_P h_P$ makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of $e_P h_P$; i.e., if increasing $e_P h_P$ increases the minimum value of r_R necessary for the resource to invade.*

2. *We say that increasing $e_P h_P$ makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of $e_P h_P$; i.e., if increasing $e_P h_P$ increases the maximum value of r_R, below which the resource will be excluded. We say that increasing $e_P h_P$ makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of $e_P h_P$; i.e., if increasing $e_P h_P$ decreases the maximum value of r_R, below which the resource is excluded.*

Theorem 4.6. *Increasing $e_P h_P$*

1. *makes it easier for the resource to invade if $\frac{1}{2} \alpha_{CP} e_{CP} K_C - m_P (1 + e_{CP} h_{CP} K_C) > 0$ and $e_{RC} \ll e_{RP}$.*

2. *makes it harder for the resource to invade if*

    (a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $e_{RC} >> e_{RP}$.

    (b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.

3. *makes it easier for the resource to be excluded if*

    (a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $e_{RC} >> e_{RP}$.

    (b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.

4. *makes it harder for the resource to be excluded if* $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $e_{RC} << e_{RP}$.

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, the first fraction on the right hand side of invasibility condition (4.37) is of the form

$$f(e_P h_P) = \frac{A e_P h_P}{B + C e_P h_P}$$

where

$$A = e_{RC}K_C$$
$$B = e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{m_P}\right]$$
$$C = 1 + \frac{1}{2}e_C h_C K_C$$

Here, $B > 0$ since we are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$. So, increasing $e_P h_P$ causes the first fraction on the right hand side of invasibility condition (4.37) to increase.

The second fraction on the right hand side of invasibility condition (4.37) is of the form

$$g(e_P h_P) = \frac{D}{e_P h_P}$$

where

$$D = \frac{2e_{RP}\alpha_{CP}}{\alpha_{CP} - h_{CP}m_P}.$$

Here, $D > 0$ because of inequality (4.10). So, increasing e_Ph_P causes the second fraction on the right hand side of invasibility condition (4.37) to decrease.

Thus, increasing e_Ph_P causes the first fraction on the right hand side of invasibility condition (4.37) to increase while causing the second fraction to decrease. When we add these fractions together, we could have that the right hand side is increasing or decreasing as a result of increasing e_Ph_P. If $e_{RC} >> e_{RP}$, then the first fraction on the right hand side will dominate the second fraction, so increasing e_Ph_P causes the right hand side to increase. This makes invasion harder. But if $e_{RC} << e_{RP}$, then the second fraction on the right hand side will dominate the first fraction, so increasing e_Ph_P causes the right hand side to decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(e_Ph_P) = \frac{Ae_Ph_P}{B + Ce_Ph_P}$$

where

$$A = \frac{1}{2}e_{RC}K_C$$
$$B = \frac{e_{CP}^2 h_{PC}K_C\alpha_{CP}}{m_P}$$
$$C = 1 + e_Ch_CK_C$$

We have that $f'(e_Ph_P) > 0$, so increasing e_Ph_P causes the first fraction on the right hand side of exclusion condition (4.38) to increase.

The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$g(e_Ph_P) = \frac{D}{e_Ph_P}$$

where

$$D = \frac{e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)\right]}{m_P(1 + e_{CP}h_{CP}K_C) + K_C\alpha_{CP}e_{CP}}$$

We have that $g'(e_P h_P) < 0$. So, increasing $e_P h_P$ causes the second fraction on the right hand side of exclusion condition (4.38) to decrease.

Therefore, increasing $e_P h_P$ causes the first fraction on the right hand side of exclusion condition (4.38) to increase, while causing the second fraction to decrease. When we add these fractions together, we get that the right hand side could be increasing or decreasing as a result of increasing $e_P h_P$. If $e_{RC} >> e_{RP}$, then the first fraction on the right hand side will dominate the second fraction. So increasing $e_P h_P$ causes the right hand side of the exclusion condition to increase, which makes exclusion easier. But if $e_{RC} << e_{RP}$, then the second fraction on the right hand side will dominate the first fraction. So increasing $e_P h_P$ causes the right hand side of the exclusion condition to decrease, which makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$, the first fraction on the right hand side of invasibility condition (4.39) is independent of $e_P h_P$, so increasing $e_P h_P$ does not change the resource's ability to invade. The second fraction on the right hand side of invasibility condition (4.39) is of the form

$$f(e_P h_P) = \frac{A}{e_P h_P}$$

where

$$A = \frac{e_{RP}K_C\alpha_{CP}e_{CP}}{m_P\left(1 + \frac{1}{2}e_{CP}h_{CP}K_C\right)}$$

We have that $f'(e_P h_P) < 0$. So, increasing $e_P h_P$ causes the right hand side of the invasibility condition to decrease, which makes invasion harder.

The right hand side of exclusion condition (4.40) is of the form

$$f(e_P h_P) = \frac{A e_P h_P}{B + C e_P h_P}$$

where

$$A = \frac{1}{2}e + RCK_C$$

$$B = \frac{e_{CP}^2 h_{PC} K_C \alpha_{CP}}{m_P}$$

$$C = 1 + e_C h_C K_C$$

We have that $f'(e_P h_P) > 0$. So, increasing $e_P h_P$ causes the right hand side of the exclusion condition to increase, which makes exclusion easier. □

□

Before stating the following theorem, we introduce some terminology.

Definition 4.5. *1. We say that increasing e_{CP} makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of e_{CP}; i.e., if increasing e_{CP} reduces the minimum value of r_R necessary for the resource to invade. We say that increasing e_{CP} makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of e_{CP}; i.e., if increasing e_{CP} increases the minimum value of r_R necessary for the resource to invade.*

2. We say that increasing e_{CP} makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of e_{CP}; i.e., if increasing e_{CP} increases the maximum value of r_R, below which the resource will be excluded. We say that increasing e_{CP} makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of e_{CP}; i.e., if increasing e_{CP} decreases the maximum value of r_R, below which the resource is excluded.

Theorem 4.7. *Increasing e_{CP}*

1. *makes it easier for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.*

2. *makes it harder for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

3. *makes it easier for the resource to be excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} \gg e_{RP}$.*

4. *makes it harder for the resource to be excluded if*

   (a) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} \ll e_{RP}$.*

   (b) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

Proof. We are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ if and only if

$$
e_{CP}
\begin{cases}
> \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C} & \text{if } \frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C > 0 \\[2mm]
< \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C} & \text{if } \frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C < 0
\end{cases}.
$$

Note that if $\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C < 0$, then we would have $e_{CP} < 0$, which we cannot have. So, we must have $e_{CP} > \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}$ with $\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C > 0$.

The second fraction on the right hand side of invasibility condition (4.37) does not depend on e_{CP} so increasing e_{CP} does not change the resource's ability to invade. We can rewrite the denominator of the first fraction as

$$
1 + \frac{e_{CP}h_{PC}}{e_P h_P m_P}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P - m_P e_{CP}h_{CP}K_C\right] + \frac{1}{2}e_C h_C K_C
$$
$$
= 1 + \frac{e_{CP}h_{PC}}{e_P h_P m_P}\left[e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right) - m_P\right] + \frac{1}{2}e_C h_C K_C
$$

So the first fraction on the right hand side of invasibility condition (4.37) is of the form

$$
f(e_{CP}) = \frac{A}{B e_{CP}^2 - C e_{CP} + D}
$$

where

$$A = e_{RC}K_C$$

$$B = \frac{h_{PC}K_C}{e_P h_P m_P}\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right)$$

$$C = \frac{h_{PC}}{e_P h_P}$$

$$D = 1 + \frac{1}{2}e_C h_C K_C$$

Here, B is positive. So we have that

$$f'(e_{CP}) = -\frac{A(2Be_{CP} - C)}{(Be_{CP}^2 - Ce_{CP} + D)^2} \begin{cases} < 0 \text{ if } e_{CP} > \frac{C}{2B} \\ \\ > 0 \text{ if } e_{CP} < \frac{C}{2B} \end{cases}$$

Note that

$$\frac{C}{2B} = \frac{m_P}{2K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right)}$$

so, in order for $f'(e_{CP}) > 0$, we must have

$$e_{CP} < \frac{m_P}{2K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right)} \Leftrightarrow 2e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right) - m_P < 0$$

$$\Leftrightarrow e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right) - \frac{1}{2}m_P < 0$$

$$\Rightarrow e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right) - m_P < 0$$

which contradicts the assumption that we are in the case where

$$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0.$$

So, we have that $f'(e_{CP}) < 0$.

Thus, increasing e_{CP} causes the right hand side of invasibility condition (4.37) to decrease, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(e_{CP}) = \frac{A}{B + Ce_{CP}^2}$$

where

$$A = \frac{1}{2}e_{RC}K_C$$

$$B = 1 + e_C h_C K_C$$

$$C = \frac{h_{PC}K_C\alpha_{CP}}{e_P h_P m_P}$$

We have that

$$f'(e_{CP}) = -\frac{2ACe_{CP}}{(B + Ce_{CP}^2)^2} < 0$$

So, increasing e_{CP} causes the first fraction on the right hand side of exclusion condition (4.38) to decrease.

The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$g(e_{CP}) = \frac{-D + Ee_{CP}}{F + Ge_{CP}}$$

where

$$D = e_{RP}m_P$$

$$E = e_{RP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right)$$

$$F = e_P h_P m_P$$

$$G = e_P h_P(m_P h_{CP} + \alpha_{CP})K_C$$

Since we are in the case where $\frac{1}{2}e_{CP}h_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - m_P h_{CP}\right) > \frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)$, then we must

have $\frac{1}{2}\alpha_{CP} - m_P h_{CP} > 0$. Thus, we have $E > 0$ in this case. We have that

$$g'(e_{CP}) = \frac{EF + DG}{(F + Ge_{CP})^2} > 0.$$

Thus, increasing e_{CP} causes the second fraction on the right hand side of exclusion condition (4.38) to increase.

Therefore, increasing e_{CP} causes the first fraction on the right hand side of exclusion condition (4.38) to decrease, while causing the second fraction to increase. When we add these fractions together, we could have that the right hand side is increasing or decreasing as a result of increasing e_{CP}. If $e_{RC} >> e_{RP}$, then the first fraction on the right hand side of exclusion condition (4.38) dominates the second fraction, so increasing e_{CP} causes the right hand side of the exclusion condition to decrease. This makes exclusion easier. But, if $e_{RC} << e_{RP}$, then the second fraction on the right hand side of exclusion condition (4.38) dominates the first fraction, so increasing e_{CP} causes the right hand side to increase. This makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{CP} e_{CP} K_C - m_P (1 + e_{CP} h_{CP} K_C) < 0$, the first fraction on the right hand side of invasibility condition (4.39) does not depend on e_{CP}. So increasing e_{CP} does not change the resource's ability to invade. The second fraction on the right hand side of the invasibility condition is of the form

$$f(e_{CP}) = \frac{Ae_{CP}}{B + Ce_{CP}}$$

where

$$A = \frac{e_{RP} K_C \alpha_{CP}}{e_P h_P m_P}$$

$$B = 1$$

$$C = \frac{1}{2} h_{CP} K_C$$

We have that $f'(e_{CP}) > 0$. So, increasing e_{CP} causes the right hand side of the invasibility condition to increase, which makes invasion harder.

The right hand side of exclusion condition (4.40) is of the form

$$f(e_{CP}) = \frac{A}{B + Ce_{CP}^2}$$

where

$$A = \frac{1}{2}e_{RC}K_C$$
$$B = 1 + e_Ch_CK_C$$
$$C = \frac{h_{PC}K_C\alpha_{CP}}{e_Ph_Pm_P}$$

We have that $f'(e_{CP}) > 0$. So, increasing e_{CP} causes the right hand side of exclusion condition (4.40) to decrease, which makes exclusion harder. □

Before stating the following theorem, we introduce some terminology.

Definition 4.6. *1. We say that increasing h_{CP} makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of h_{CP}; i.e., if increasing h_{CP} reduces the minimum value of r_R necessary for the resource to invade. We say that increasing h_{CP} makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of h_{CP}; i.e., if increasing h_{CP} increases the minimum value of r_R necessary for the resource to invade.*

2. We say that increasing h_{CP} makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of h_{CP}; i.e., if increasing h_{CP} increases the maximum value of r_R, below which the resource will be excluded. We say that increasing h_{CP} makes it harder for the resource to be excluded if the right hand side of either exclusion

condition (4.38) or (4.40) is a decreasing function of h_{CP}; i.e., if increasing h_{CP} decreases the maximum value of r_R, below which the resource is excluded.

Theorem 4.8. *Increasing h_{CP}*

1. *makes it easier for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

2. *makes it harder for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.*

3. *makes it harder for the resource to be excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.*

4. *has no effect on whether the resource is excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.*

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, which is the case if $h_{CP} < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P}{e_{CP}K_C m_P}$, the first fraction on the right hand side of invasibility condition (4.37) is of the form

$$f(h_{CP}) = \frac{A}{B - Ch_{CP}}$$

where

$$A = e_{RC}K_C$$
$$B = 1 + \frac{1}{2}e_C h_C K_C + \frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{2e_P h_P m_P} - \frac{1}{e_P h_P}$$
$$C = \frac{e_{CP}^2 h_{PC}K_C}{e_P h_P}$$

Here, B could be positive or negative. We have that

$$f'(h_{CP}) = \frac{AC}{(B - Ch_{CP})^2} > 0.$$

So, increasing h_{CP} causes the first fraction on the right hand side of invasibility condition (4.37) to increase.

The second fraction on the right hand side of invasibility condition (4.37) is of the form

$$g(h_{CP}) = \frac{D}{E - Fh_{CP}}$$

where

$$D = 2e_{RP}\alpha_{CP}$$

$$E = e_P h_P \alpha_{CP}$$

$$F = e_P h_P m_P$$

We have that $g'(h_{CP}) > 0$. So, increasing h_{CP} causes the second fraction on the right hand side of invasibility condition (4.37) to increase.

So, increasing h_{CP} causes both the first and second fraction on the right hand side of the invasibility condition to increase. When we add these fractions together, we get that the right hand side of invasibility condition (4.37) is increasing as a result of increasing h_{CP}. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.38) does not depend on h_{CP}, so increasing h_{CP} does not change the possibility of the resource being excluded from the system. The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(h_{CP}) = \frac{A - Bh_{CP}}{C + Dh_{CP}}$$

where

$$A = e_{RP}\left(\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\right)$$

$$B = e_{RP}e_{CP}K_C m_P$$

$$C = e_{Ph_P}m_P + K_C\alpha_{CP}e_{CP}e_{Ph_P}$$

$$D = e_{Ph_P}m_P e_{CP}K_C$$

Since we are in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < \frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P$, then we must have $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P > 0$. Therefore, $A > 0$. We have that

$$f'(h_{CP}) = -\frac{BC + AD}{(C + Dh_{CP})^2} < 0.$$

So, increasing h_{CP} causes the right hand side of exclusion condition (4.38) to decrease, which makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}K_C\right) < 0$, the first fraction on the right hand side of invasibility condition (4.39) does not depend on h_{CP}, so increasing h_{CP} does not change the resource's ability to invade. The second fraction on the right hand side of invasibility condition (4.39) is of the form

$$f(h_{CP}) = \frac{A}{B + Ch_{CP}}$$

where

$$A = \frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_{Ph_P}m_P}$$

$$B = 1$$

$$C = \frac{1}{2}e_{CP}K_C$$

We have that $f'(h_{CP}) > 0$, so increasing h_{CP} causes the right hand side of invasibility condition (4.39) to decrease. This makes invasion easier.

The right hand side of exclusion condition (4.40) does not depend on h_{CP}, so increasing h_{CP} does not change whether the resource will be excluded. $\qquad\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.7. *1. We say that increasing h_{PC} makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of h_{PC}; i.e., if increasing h_{PC} reduces the minimum value of r_R necessary for the resource to invade. We say that increasing h_{PC} makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of h_{PC}; i.e., if increasing h_{PC} increases the minimum value of r_R necessary for the resource to invade.*

2. We say that increasing h_{PC} makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of h_{PC}; i.e., if increasing h_{PC} increases the maximum value of r_R, below which the resource will be excluded. We say that increasing h_{PC} makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of h_{PC}; i.e., if increasing h_{PC} decreases the maximum value of r_R, below which the resource is excluded.

Theorem 4.9. *Increasing h_{PC}*

1. makes it easier for the resource to invade if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.

2. makes it harder for the resource to be excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$.

3. *makes it harder for the resource to be excluded if* $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0.$

4. *has no effect on whether the resource can invade the system if* $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0.$

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, the second fraction on the right hand side of invasibility condition (4.37) does not depend on h_{PC}. The first fraction on the right hand side of the invasibility condition is of the form

$$f(h_{PC}) = \frac{A}{B + Ch_{PC}}$$

where

$$A = e_{RC}K_C$$
$$B = 1 + \frac{1}{2}e_Ch_CK_C$$
$$C = e_{CP}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{e_Ph_Pm_P}\right]$$

We have that $f'(h_{PC}) < 0$, so increasing h_{PC} causes the right hand side of invasibility condition (4.37) to decrease. This makes invasion easier.

The second fraction on the right hand side of exclusion condition (4.38) does not depend on h_{PC}, so increasing h_{PC} does not change whether or not the resource will be excluded. The first fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(h_{PC}) = \frac{A}{B + Ch_{PC}}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = 1 + e_C h_C K_C$$

$$C = \frac{e_{CP}^2 K_C \alpha_{CP}}{e_P h_P m_P}$$

We have that $f'(h_{PC}) < 0$. So, increasing h_{PC} causes the right hand side of exclusion condition (4.38) to decrease, which makes exclusion harder.

In the case where $\frac{1}{2} \alpha_{CP} e_{CP} K_C - m_P (1 + e_{CP} h_{CP} K_C) < 0$, the right hand side of invasibility condition (4.39) does not depend on h_{PC}, so increasing h_{PC} does not change the resource's ability to invade the system.

The right hand side of exclusion condition (4.40) is of the form

$$f(h_{PC}) = \frac{A}{B + C h_{PC}}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = 1 + e_C h_C K_C$$

$$C = \frac{e_{CP}^2 K_C \alpha_{CP}}{e_P h_P m_P}$$

We have that $f'(h_{PC}) > 0$. So, increasing h_{PC} causes the right hand side of exclusion condition (4.40) to decrease, which makes exclusion harder. □

Before stating the following theorem, we introduce some terminology.

Definition 4.8. *1. We say that increasing α_{CP} makes it easier for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is a decreasing function of α_{CP}; i.e., if increasing α_{CP} reduces the minimum value*

of r_R necessary for the resource to invade. We say that increasing α_{CP} makes it harder for the resource to invade if the right hand side of either invasibility condition (4.37) or (4.39) is an increasing function of α_{CP}; i.e., if increasing α_{CP} increases the minimum value of r_R necessary for the resource to invade.

2. *We say that increasing α_{CP} makes it easier for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is an increasing function of α_{CP}; i.e., if increasing α_{CP} increases the maximum value of r_R, below which the resource will be excluded. We say that increasing α_{CP} makes it harder for the resource to be excluded if the right hand side of either exclusion condition (4.38) or (4.40) is a decreasing function of α_{CP}; i.e., if increasing α_{CP} decreases the maximum value of r_R, below which the resource is excluded.*

Theorem 4.10. *Increasing α_{CP}*

1. *makes it easier for the resource to invade if*

   (a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $1 + \frac{1}{2}e_C h_C K_C > \frac{e_{CP}h_{PC}(1+e_{CP}h_{CP}K_C)}{e_P h_P}$.

   (b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1+e_{CP}h_{CP}K_C) > 0$, $1 + \frac{1}{2}e_C h_C K_C < \frac{e_{CP}h_{PC}(1+e_{CP}h_{CP}K_C)}{e_P h_P}$, *and* $e_{RC} \ll e_{RP}$.

2. *makes it harder for the resource to invade if*

   (a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1+e_{CP}h_{CP}K_C) > 0$, $1 + \frac{1}{2}e_C h_C K_C < \frac{e_{CP}h_{PC}(1+e_{CP}h_{CP}K_C)}{e_P h_P}$, *and* $e_{RC} \gg e_{RP}$.

   (b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.

3. *makes it easier for the resource to be excluded if* $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $e_{RC} \ll e_{RP}$.

4. *makes it harder for the resource to be excluded if*

(a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ *and* $e_{RC} >> e_{RP}$.

(b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$.

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$, the first fraction on the right hand side of invasibility condition (4.37) is of the form

$$f(\alpha_{CP}) = \frac{A}{B + C\alpha_{CP}}$$

where

$$A = e_{RC}K_C$$

$$B = 1 + \frac{1}{2}e_C h_C K_C - \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_P h_P}$$

$$C = \frac{e_{CP}^2 h_{PC}K_C}{2e_P h_P m_P}$$

Here, B could be positive or negative. We have that

$$f'(\alpha_{CP}) = -\frac{AB}{(B + C\alpha_{CP})^2} \begin{cases} > 0 \text{ if } B < 0 \\ \\ < 0 \text{ if } B > 0 \end{cases}$$

So, if $1 + \frac{1}{2}e_C h_C K_C < \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_P h_P}$ then increasing α_{CP} causes the first fraction on the right hand side of invasibility condition (4.37) to increase. But if $1 + \frac{1}{2}e_C h_C K_C > \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_P h_P}$, then increasing α_{CP} causes the first fraction on the right hand side of invasibility condition (4.37) to decrease.

The second fraction on the right hand side of invasibility condition (4.37) is of the form

$$g(\alpha_{CP}) = \frac{D\alpha_{CP}}{E\alpha_{CP} - F}$$

where

$$D = 2e_{RP}$$

$$E = e_P h_P$$

$$F = e_P h_P h_{CP} m_P$$

We have that

$$g'(\alpha_{CP}) = -\frac{DF}{(E\alpha_{CP} - F)^2} < 0$$

So, increasing α_{CP} causes the second fraction on the right hand side of invasibility condition (4.37) to decrease.

Therefore, if $1 + \frac{1}{2}e_C h_C K_C < \frac{e_{CP}h_{PC}(1+e_{CP}h_{CP}K_C)}{e_P h_P}$, then increasing α_{CP} causes the first fraction on the right hand side of invasibility condition (4.37) to increase while causing the second fraction to decrease. When we add these fractions together, we can have that the right hand side of invasibility condition (4.37) increases or decreases as a result of increasing α_{CP}. If $e_{RC} >> e_{RP}$, then the first fraction on the right hand side dominates the second fraction, so increasing α_{CP} causes the right hand side to increase. This makes invasion harder. But if $e_{RC} << e_{RP}$ then the second fraction on the right hand side dominates the first fraction, so increasing α_{CP} causes the right hand side to decrease. This makes invasion easier. But if $1 + \frac{1}{2}e_C h_C K_C > \frac{e_{CP}h_{PC}(1+e_{CP}h_{CP}K_C)}{e_P h_P}$ then increasing α_{CP} causes both the first fraction and the second fraction on the right hand side of invasibility condition (4.37) to decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.38) is of the form

$$f(\alpha_{CP}) = \frac{A}{B + C\alpha_{CP}}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = 1 + e_C h_C K_C$$

$$C = \frac{e_{CP}^2 h_{PC} K_C}{e_P h_P m_P}$$

We have that $f'(\alpha_{CP}) < 0$. So, increasing α_{CP} causes the first fraction on the right hand side of exclusion condition (4.38) to decrease.

The second fraction on the right hand side of exclusion condition (4.38) is of the form

$$g(\alpha_{CP}) = \frac{-D + E\alpha_{CP}}{F + G\alpha_{CP}}$$

where

$$D = e_{RP} m_P (1 + e_{CP} h_{CP} K_C)$$

$$E = \frac{1}{2} e_{RP} e_{CP} K_C$$

$$F = e_P h_P m_P (1 + e_{CP} h_{CP} K_C)$$

$$G = K_C e_{CP} e_P h_P$$

We have that

$$g'(\alpha_{CP}) = \frac{EF + DG}{(F + G\alpha_{CP})^2} > 0.$$

So, increasing α_{CP} causes the second fraction on the right hand side of exclusion condition (4.38) to increase.

Thus, increasing α_{CP} causes the first fraction on the right hand side of exclusion condition (4.38) to decrease, while causing the second fraction to increase. When we add these fractions together, it could be the case that the right hand side is increasing or decreasing as a result of increasing α_{CP}. If $e_{RC} >> e_{RP}$, then the first fraction on

the right hand side dominates the second fraction, so increasing α_{CP} causes the right hand side of exclusion condition (4.38) to decrease. This makes exclusion harder. But, if $e_{RC} << e_{RP}$, then the second fraction on the right hand side of the exclusion condition dominates the first fraction, so increasing α_{CP} causes the right hand side of the exclusion condition to increase. This makes exclusion easier.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$, the first fraction on the right hand side of invasibility condition (4.39) does not depend on α_{CP}, so increasing α_{CP} does not change the resource's ability to invade. The second fraction on the right hand side is of the form

$$f(\alpha_{CP}) = A\alpha_{CP}$$

where

$$A = \frac{e_{RP}K_Ce_{CP}}{e_Ph_Pm_P\left(1 + \frac{1}{2}e_{CP}h_{CP}K_C\right)}$$

We have that $f'(\alpha_{CP}) > 0$, so increasing α_{CP} causes the right hand side of invasibility condition (4.39) to increase. This makes invasion harder.

The right hand side of exclusion condition (4.40) is of the form

$$f(\alpha_{CP}) = \frac{A}{B + C\alpha_{CP}}$$

where

$$A = \frac{1}{2}e_{RC}K_C$$

$$B = 1 + e_Ch_CK_C$$

$$C = \frac{e_{CP}^2h_{PC}K_C}{e_Ph_Pm_P}$$

We have that $f'(\alpha_{CP}) < 0$. So, increasing α_{CP} causes the right hand side of exclusion condition (4.40) to decrease, which makes exclusion harder. $\square$

Boundary Limit Cycle

Now suppose $\alpha_{CP}e_{CP}K_C > m_P(1 + e_{CP}h_{CP}K_C)$, $(e_{CP}h_{CP}K_C - 1)(\alpha_{CP} - m_Ph_{CP}) - 2m_Ph_{CP} > 0$, e_Ph_P sufficiently small, and $\alpha_{CP}e_{CP}K_C$ sufficiently large. Then according to [14], we have the ω-periodic solution $(0, \phi_C, \phi_P)$, which is stable in the (C, P)-plane. The Floquet multiplier in the R direction is given by

$$\exp\left[\frac{1}{\omega}\int_0^\omega \left(r_R - \frac{e_{RC}\phi_C(t)}{1 + h_{PCP}\phi_P(t) + h_C\phi_C(t)} - \frac{e_{RP}\phi_P(t)}{1 + h_{CP}\phi_C(t) + \phi_P(t)}\right)dt\right].$$

Thus, if (in dimensionalized terms)

$$r_R > \int_0^\omega \left(\frac{e_{RC}\phi_C(t)}{1 + e_{CP}h_{PC}\phi_P(t) + e_Ch_C\phi_C(t)} + \frac{e_{RP}\phi_P(t)}{1 + e_{CP}h_{CP}\phi_C(t) + e_Ph_P\phi_P(t)}\right)dt \tag{4.41}$$

then $(0, \phi_C, \phi_P)$ is unstable in the R direction.

4.7 Invasibility & Exclusion when Consumers Absent

Assume $\alpha_{RP}e_{RP}K_R > (e_{RP}h_{RP}K_R + 1)m_P$. Then (R^*, P^*) exists in the (R, P)-plane and the resource-predator subsystem is permanent. Assume further that $e_{RP}h_{RP}K_R(1 - R^*) < 1$ so that (R^*, P^*) is globally asymptotically stable. If we linearize the C equation about the equilibrium (R^*, P^*), we get

$$\frac{dC}{dt} = \left(r_C + \frac{\alpha_{RC}R^*}{1 + h_{RC}R^* + h_{CPP}P^*} - \frac{e_{CP}P^*}{1 + h_{RP}R^* + P^*}\right)C. \tag{4.42}$$

In order for the basal resource to invade the system, we need $\frac{dC}{dt} > 0$, which gives us (in dimensionalized terms)

$$r_C > \frac{e_{CP}P^*}{1 + e_{RP}h_{RP}R^* + e_Ph_PP^*} - \frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^* + e_{CP}h_{CP}P^*}. \tag{4.43}$$

If we have that

$$r_C < \frac{e_{CP}P^*}{1 + e_{RP}h_{RP}R^* + e_P h_P P^*} - \frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^* + e_{CP}h_{CP}P^*} \qquad (4.44)$$

then the consumer will be excluded from the system. If we use the bounds on R^* and P^* given by inequalities (4.21) and (4.22), then we get two possibilities depending on whether $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ or $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$. If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ then invasibility condition (4.43) becomes

$$r_C > \frac{\frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{m_P}}$$
$$- \frac{\frac{1}{2}\alpha_{RC}e_{RC}K_R}{1 + e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}}. \qquad (4.45)$$

We can simplify the denominator of the first fraction to get

$$1 + \frac{1}{2}e_{RP}h_{RP}K_R + \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{m_P}$$
$$= 1 + \frac{1}{2}e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{2m_P} - 1 - e_{RP}h_{RP}K_R$$
$$= \frac{1}{2}e_{RP}K_R\left(\frac{\alpha_{RP}}{m_P} - h_{RP}\right)$$

Thus, the first fraction becomes

$$\frac{\frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{m_P}} = \frac{\frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}}{\frac{1}{2}e_{RP}K_R\left(\frac{\alpha_{RP}}{m_P} - h_{RP}\right)}$$
$$= \frac{2e_{CP}\alpha_{RP}}{e_P h_P(\alpha_{RP} - m_P h_{RP})}$$

So, if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ then invasibility condition (4.43)

becomes

$$r_C > \frac{2e_{CP}\alpha_{RP}}{e_P h_P(\alpha_{RP} - m_P h_{RP})} - \frac{\frac{1}{2}\alpha_{RC}e_{RC}K_R}{1 + e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}} \tag{4.46}$$

and exclusion condition (4.44) becomes

$$r_C < \frac{\frac{e_{CP}\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)\right]}{e_P h_P m_P}}{1 + e_{RP}h_{RP}K_R + \frac{K_R\alpha_{RP}e_{RP}}{m_P}}$$
$$- \frac{\alpha_{RC}e_{RC}K_R}{1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_{CP}h_{CP}\left[\frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{e_P h_P m_P}\right]}. \tag{4.47}$$

Biological Remarks:

(i) If $\frac{\alpha_{RP}}{h_{RP}} < m_P$, then the resource will always be able to invade. In this case, the predator does not gain much by consuming the resource compared to the amount of time it spends handling the resource, so if there is a sufficient amount of resource or the predators naturally die at a sufficiently high rate, then their inefficiency will keep their population density too low to be able to stop the consumers from invading.

(ii) Even if $\frac{\alpha_{RP}}{h_{RP}} > m_P$, it could still be the case that the consumer can invade if

$$\frac{\frac{1}{2}\alpha_{RC}e_{RC}K_R}{1 + e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}} > \frac{2e_{CP}\alpha_{RP}}{e_P h_P(\alpha_{RP} - m_P h_{RP})}.$$

One way in which this could happen is if $\alpha_{RC}e_{RC}$ is sufficiently large; i.e., if the consumer gains sufficiently from consuming the resource. Another way in which this could happen is if $e_P h_P$ is sufficiently large; i.e., if the predators interfere with each other sufficiently.

(iii) If

$$\frac{\alpha_{RC}e_{RC}K_R}{1+\frac{1}{2}e_{RC}h_{RC}K_R + e_{CP}h_{CP}\left[\frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1+e_{RP}h_{RP}K_R)}{e_Ph_Pm_P}\right]}$$
$$> \frac{\frac{e_{CP}\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1+e_{RP}h_{RP}K_R)\right]}{e_Ph_Pm_P}}{1+e_{RP}h_{RP}K_R + \frac{K_R\alpha_{RP}e_{RP}}{m_P}}$$

then the consumers cannot be excluded from the system. One way in which this could happen is if e_Ph_P is sufficiently large; i.e., if the predators interfere with each other sufficiently. Another way in which this could happen is if e_{CP} is sufficiently small; i.e., if the predators encounter the consumers at a sufficiently low rate. A third way in which this could happen is if α_{RC} is sufficiently large; i.e., the consumers gain sufficiently from consuming the resource.

If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1+h_{RP}e_{RP}K_R) < 0$ then the invasibility condition becomes

$$r_C > \frac{\frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_Ph_Pm_P}}{1+\frac{1}{2}e_{RP}h_{RP}K_R} - \frac{\frac{1}{2}\alpha_{RC}e_{RC}K_R}{1+e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_Ph_Pm_P}} \tag{4.48}$$

and the exclusion condition becomes

$$r_C < -\frac{\alpha_{RC}e_{RC}K_R}{1+\frac{1}{2}e_{RC}h_{RC}K_R}. \tag{4.49}$$

Biological Remarks:

(i) If

$$\frac{\frac{1}{2}\alpha_{RC}e_{RC}}{1+e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_Ph_Pm_P}} > \frac{\frac{e_{CP}\alpha_{RP}e_{RP}}{e_Ph_Pm_P}}{1+\frac{1}{2}e_{RP}h_{RC}K_R}$$

then the consumers will always be able to invade. One way in which this could happen is if $\alpha_{RC} >> \alpha_{RP}$; i.e., if the consumers gain much more from consuming the resource than the predators do. Another way in which this could happen is if $e_Ph_Pm_P$ is sufficiently large; i.e., if the predators interfere with each other a

sufficient amount or if the predators have a sufficiently high natural mortality rate. A third way in which this could happen is if h_{RP} is sufficiently large; i.e., if the predators spend a sufficiently large amount of time handling encountered resource. Yet another way in which this could happen is if e_{CP} is sufficiently small; i.e., if the predators do not attack the consumers often.

(ii) In this case, the consumers cannot be excluded. This is to be expected though. In order to be in this case, the predators have some combination of gaining sufficiently little from consuming the resource, spending a sufficiently large amount of time handling encountered resource, and/or a sufficiently high natural mortality rate. The combination of these factors limits the predators' growth rate, which limits the predators' ability to exclude the consumers.

Note that whether the consumer is able to invade or is excluded from the system depends in part on parameters which are independent of the consumer itself.

Before stating the following theorem, we introduce some terminology.

Definition 4.9. *1. We say that increasing K_R makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of K_R; i.e., if increasing K_R reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing K_R makes it harder for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is an increasing function of K_R; i.e., if increasing K_R increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing K_R makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of K_R; i.e., if increasing K_R increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing K_R makes it harder for the consumers to be excluded if the right hand side of either exclusion

condition (4.47) or (4.49) is a decreasing function of K_R; i.e., if increasing K_R decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.11. *Increasing K_R*

1. *makes it easier for the consumer to invade if*

    (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.

    (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$ *and* $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$.

2. *makes it harder for the consumer to invade if* $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$ *and* $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$.

3. *makes it easier for the consumer to be excluded if*

    (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ *and* $e_{CP}h_{CP} > e_Ph_P$.

    (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, $e_{CP}h_{CP} < e_Ph_P$, *and* $e_{CP} >> e_{RC}$.

4. *makes it harder for the consumer to be excluded if* $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, $e_{CP}h_{CP} < e_Ph_P$, *and* $e_{CP} << e_{RC}$.

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, the first fraction on the right hand side of invasibility condition (4.46) is independent of K_R. The second fraction on the right hand side of invasibility condition (4.46) is of the form

$$g(K_R) = \frac{DK_R}{E + FK_R}$$

where

$$D = \frac{1}{2}\alpha_{RC}e_{RC}$$

$$E = 1$$

$$F = e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_Ph_Pm_P}$$

We have that

$$g'(K_R) = \frac{DE}{(E + FK_R)^2} > 0.$$

Thus, increasing K_R increases the second fraction on the right hand side of invasibility condition (4.46). But since we are subtracting this second fraction on the right hand side of invasibility condition (4.46), we get that increasing K_R causes the right hand side of invasibility condition (4.46) to decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.47) is of the form

$$f(K_R) = \frac{-A + BK_R}{C + DK_R}$$

where

$$A = \frac{e_{CP}}{e_P h_P}$$

$$B = \frac{e_{CP} \left(\frac{1}{2}\alpha_{RP}e_{RP} - m_P e_{RP} h_{RP}\right)}{e_P h_P m_P}$$

$$C = 1$$

$$D = e_{RP} h_{RP} + \frac{\alpha_{RP} e_{RP}}{m_P}$$

Since we are in the case where $\frac{1}{2}\alpha_{RP}e_{RP} - m_P(1 + h_{RP}e_{RP}K_R) > 0$ and $\frac{1}{2}\alpha_{RP}e_{RP} - m_P(1 + h_{RP}e_{RP}K_R) < \frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P e_{RP}h_{RP}K_R = K_R\left(\frac{1}{2}\alpha_{RP}e_{RP} - m_P e_{RP}h_{RP}\right)$, then we have that $B > 0$. We also have that

$$f'(K_R) = \frac{BC + AD}{(C + DK_R)^2} > 0.$$

So, increasing K_R causes the first fraction on the right hand side of exclusion condition (4.47) to increase.

The second fraction on the right hand side of exclusion condition (4.47) is of the

form

$$g(K_R) = \frac{EK_R}{F + GK_R}$$

where

$$E = \alpha_{RC} e_{RC}$$

$$F = 1 - \frac{e_{CP} h_{CP}}{e_P h_P}$$

$$G = \frac{1}{2} e_{RC} h_{RC} + e_{CP} h_{CP} \left(\frac{\frac{1}{2} \alpha_{RP} e_{RP} - m_P e_{RP} h_{RP}}{e_P h_P m_P} \right)$$

We have that

$$g'(K_R) = \frac{EF}{(F + GK_R)^2} \begin{cases} > 0 \text{ if } F > 0 \\ \\ < 0 \text{ if } F < 0 \end{cases}.$$

So, if $e_{CP} h_{CP} < e_P h_P$ then increasing K_R causes the second fraction on the right hand side of exclusion condition (4.47) to increase. And if $e_{CP} h_{CP} > e_P h_P$ then increasing K_R causes the second fraction on the right hand side of exclusion condition (4.47) to decrease.

Thus, if $e_{CP} h_{CP} < e_P h_P$ then increasing K_R causes both the first and second fractions on the right hand side of exclusion condition (4.47) to increase. But since we are subtracting the second fraction, the right hand side of the exclusion condition could be increasing or decreasing as a result of increasing K_R. If $e_{CP} >> e_{RC}$ then the first fraction on the right hand side dominates the second fraction. In this case, increasing K_R causes the right hand side of exclusion condition (4.47) to increase. This makes exclusion easier. And if $e_{CP} << e_{RC}$ then the second fraction on the right hand side dominates the first fraction. In this case, increasing K_R cause the right hand side of the exclusion condition to decrease. This makes exclusion harder. But, if $e_{CP} h_{CP} > e_P h_P$ then increasing K_R causes the first fraction on the right hand side of exclusion condition (4.47) to increase while causing the second fraction

to decrease. But since we are subtracting the second fraction, then increasing K_R causes the right hand side of exclusion condition (4.46) to increase. This makes exclusion easier.

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$, the first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(K_R) = \frac{AK_R}{B + CK_R}$$

where

$$A = \frac{e_{CP}\alpha_{RP}e_{RP}}{e_P h_P m_P}$$

$$B = 1$$

$$C = \frac{1}{2}e_{RP}h_{RP}$$

We have that $f'(K_R) > 0$. Thus, increasing K_R causes the first fraction on the right hand side of invasibility condition (4.48) to increase.

The second fraction on the right hand side of invasibility condition (4.48) is of the form

$$g(K_R) = \frac{DK_R}{E + FK_R}$$

where

$$D = \frac{1}{2}\alpha_{RC}e_{RC}$$

$$E = 1$$

$$F = e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_P h_P m_P}$$

We have that $g'(K_R) > 0$. Thus, increasing K_R causes the second fraction on the right hand side of invasibility condition (4.48) to increase. But since we are subtracting

the second fraction, increasing the second fraction will cause the right hand side of the invasibility condition to decrease.

So, increasing K_R causes the first fraction on the right hand side of invasibility condition (4.48) to increase, while causing the second fraction to make the right hand side decrease. When we add these fractions together, it could be the case that the right hand side of invasibility condition (4.48) is increasing or decreasing as a result of increasing K_R. If $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$, then the first fraction on the right hand side of invasibility condition (4.48) will dominate the second fraction. This means that increasing K_R will cause the right hand side to increase, which makes invasibility harder. But, if $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$, then the second fraction on the right hand side of invasibility condition (4.48) will dominate the first fraction. This means that increasing K_R will cause the right hand side to decrease, which makes invasibility easier. □

Before stating the following theorem, we introduce some terminology.

Definition 4.10. *1. We say that increasing α_{RP} makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of α_{RP}; i.e., if increasing α_{RP} reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing α_{RP} makes it harder for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is an increasing function of α_{RP}; i.e., if increasing α_{RP} increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing α_{RP} makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of α_{RP}; i.e., if increasing α_{RP} increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing α_{RP} makes it harder for the consumers to be excluded if the right hand side of either exclusion

condition (4.47) or (4.49) is a decreasing function of α_{RP}; i.e., if increasing α_{RP} decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.12. *Increasing α_{RP}*

1. *makes invasion easier if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ and $2e_{CP}\alpha_{RP} >> \frac{1}{2}\alpha_{RC}e_{RC}$.*

2. *makes invasion harder if*

   (a) *$\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ and $2e_{CP}\alpha_{RP} << \frac{1}{2}\alpha_{RC}e_{RC}$.*

   (b) *$\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$.*

3. *makes exclusion easier if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.*

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, the first fraction on the right hand side of invasibility condition (4.46) is of the form

$$f(\alpha_{RP}) = \frac{A\alpha_{RP}}{B\alpha_{RP} - C}$$

where

$$A = 2e_{CP}$$
$$B = e_P h_P$$
$$C = e_P h_P m_P h_{RP}$$

We have that

$$f'(\alpha_{RP}) = -\frac{AC}{(B\alpha_{RP} - C)^2} < 0$$

So, increasing α_{RP} causes the first fraction on the right hand side of invasibility condition (4.46) to decrease.

The second fraction on the right hand side of invasibility condition (4.46) is of the form

$$g(\alpha_{RP}) = \frac{D}{E + F\alpha_{RP}}$$

where

$$D = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$E = 1 + e_{RC}h_{RC}K_R$$

$$F = \frac{e_{CP}h_{CP}K_Re_{RP}}{e_Ph_Pm_P}$$

We have that

$$g'(\alpha_{RP}) = -\frac{DE}{(E + F\alpha_{RP})^2} < 0$$

So, increasing α_{RP} causes the second fraction on the right hand side of invasibility condition (4.46) to increase. But since we are subtracting the second fraction, decreasing the second fraction causes the right hand side to increase.

So, increasing α_{RP} causes the first fraction on the right hand side of the invasibility condition to decrease, while causing the second fraction to make the right hand side increase. When we add these fractions together, we get that the right hand side of the invasibility condition could be increasing or decreasing as a result of increasing α_{RP}. If $2e_{CP}\alpha_{RP} >> \frac{1}{2}\alpha_{RC}e_{RC}$ then the first fraction on the right hand side of invasibility condition (4.46) dominates the second fraction. In this case, increasing α_{RP} causes the right hand side to decrease, which makes invasion easier. But, if $2e_{CP}\alpha_{RP} << \frac{1}{2}\alpha_{RC}e_{RC}$ then the second fraction on the right hand side of invasibility condition (4.46) dominates the first fraction. In this case, increasing α_{RP} causes the right hand side to increase, which makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.47) is of the

form

$$f(\alpha_{RP}) = \frac{-A + B\alpha_{RP}}{C + D\alpha_{RP}}$$

where

$$A = \frac{e_{CP}m_P(1 + e_{RP}h_{RP}K_R)}{e_P h_P m_P}$$

$$B = \frac{e_{CP}e_{RP}K_R}{2e_P h_P m_P}$$

$$C = 1 + e_{RP}h_{RP}K_R$$

$$D = \frac{K_R e_{RP}}{m_P}$$

We have that

$$f'(\alpha_{RP}) = \frac{BC + AD}{(C + D\alpha_{RP})^2} > 0$$

So, increasing α_{RP} causes the first fraction on the right hand side of exclusion condition (4.47) to increase.

The second fraction on the right hand side of exclusion condition (4.47) is of the form

$$g(\alpha_{RP}) = \frac{E}{F + G\alpha_{RP}}$$

where

$$E = \alpha_{RC}e_{RC}K_R$$

$$F = 1 + \frac{1}{2}e_{RC}h_{RC}K_R - \frac{e_{CP}h_{CP}m_P(1 + e_{RP}h_{RP}K_R)}{e_P h_P m_P}$$

$$G = \frac{e_{CP}h_{CP}e_{RP}K_R}{2e_P h_P m_P}$$

Here, F could be positive or negative. We have that

$$f'(\alpha_{RP}) = -\frac{EG}{(F + G\alpha_{RP})^2} < 0$$

So, increasing α_{RP} causes the second fraction on the right hand side of exclusion condition (4.47) to decrease. But since we are subtracting the second fraction, decreasing the second fraction causes the right hand side to increase.

Thus, increasing α_{RP} means that both the first fraction and second fraction on the right hand side of exclusion condition (4.47) cause the right hand side increase, which makes exclusion easier.

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$, the first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(\alpha_{RP}) = A\alpha_{RP}$$

where

$$A = \frac{e_{CP}K_R\alpha_{RP}}{e_Ph_Pm_P\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R\right)}$$

We have that $f'(\alpha_{RP}) > 0$, so increasing α_{RP} causes the first fraction on the right hand side of invasibility condition (4.48) to increase.

The second fraction on the right hand side of invasibility condition (4.48) is of the form

$$g(\alpha_{RP}) = \frac{B}{C + D\alpha_{RP}}$$

where

$$B = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$C = 1 + e_{RC}h_{RC}K_R$$

$$D = \frac{e_{CP}h_{CP}K_Re_{RP}}{e_Ph_Pm_P}$$

We have that $g'(\alpha_{PR}) > 0$. So, increasing α_{RP} causes the second fraction on the right hand side of invasibility condition (4.48) to decrease. But, since we are subtracting the second fraction, decreasing the second fraction causes the right hand side of

invasibility condition (4.48) to increase.

Thus, increasing α_{RP} causes both the first fraction and second fraction on the right hand side of invasibility condition (4.48) to make the right hand side increase. This makes invasion harder. □

Before stating the following theorem, we introduce some terminology.

Definition 4.11.   *1. We say that increasing m_P makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of m_P; i.e., if increasing m_P reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing m_P makes it harder for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is an increasing function of m_P; i.e., if increasing m_P increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing m_P makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of m_P; i.e., if increasing m_P increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing m_P makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is a decreasing function of m_P; i.e., if increasing m_P decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.13. *Increasing m_P*

1. makes invasion easier if

  (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ and $2e_{CP}\alpha_{RP} << \frac{1}{2}\alpha_{RC}e_{RC}$.

  (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$.

2. makes invasion harder if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$ and $2e_{CP}\alpha_{RP} >> \frac{1}{2}\alpha_{RC}e_{RC}$.

3. *makes exclusion harder if* $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, which is equivalent to $m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1+e_{RP}h_{RP}K_R}$, the first fraction on the right hand side of invasibility condition (4.46) is of the form

$$f(m_P) = \frac{A}{B - Cm_P}$$

where

$$A = 2e_{CP}\alpha_{RP}$$

$$B = e_{Ph}p\alpha_{RP}$$

$$C = e_{Ph}p h_{RP}$$

We have that

$$f'(m_P) = \frac{AC}{(B - Cm_P)^2} > 0$$

So, increasing m_P causes the first fraction on the right hand side of invasibility condition (4.46) to increase.

The second fraction on the right hand side of invasibility condition (4.46) is of the form

$$g(m_P) = \frac{Dm_P}{E + Fm_P}$$

where

$$D = \frac{1}{2}\alpha_{RC}e_{RC}K_R e_{Ph}p$$

$$E = e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}$$

$$F = e_{Ph}p(1 + e_{RC}h_{RC}K_R)$$

We have that

$$g'(m_P) = \frac{DE}{(E + Fm_P)^2} > 0$$

So, increasing m_P causes the second fraction on the right hand side of invasibility condition (4.46) to increase. But, since we are subtracting the second fraction on the right hand side of invasibility condition (4.46), increasing the second fraction causes the right hand side to decrease.

Therefore, increasing m_P causes the first fraction on the right hand side of invasibility condition (4.46) to increase, while causing the second fraction to make the right hand side decrease. When we add these fractions together, we get that the right hand side of the invasibility condition could be increasing or decreasing as a result of increasing m_P. If $2e_{CP}\alpha_{RP} >> \frac{1}{2}\alpha_{RC}e_{RC}$ then the first fraction on the right hand side of invasibility condition (4.46) dominates the second fraction, so increasing m_P causes the right hand side to increase. This makes invasion harder. But, if $2e_{CP}\alpha_{RP} << \frac{1}{2}\alpha_{RC}e_{RC}$ then the second fraction on the right hand side of invasibility condition (4.46) dominates the first fraction, so increasing m_P causes the right hand side to decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.47) is of the form

$$f(m_P) = \frac{A - Bm_P}{C + Dm_P}$$

where

$$A = \frac{e_{CP}\alpha_{RP}e_{RP}K_R}{2e_P h_P}$$
$$B = \frac{e_{CP}(1 + e_{RP}h_{RP}K_R)}{e_P h_P}$$
$$C = K_R\alpha_{RP}e_{RP}$$
$$D = 1 + e_{RP}h_{RP}K_R$$

We have that

$$f'(m_P) = -\frac{BC + AD}{(C + Dm_P)^2} < 0$$

So, increasing m_P causes the first fraction on the right hand side of exclusion condition (4.47) to decrease.

The second fraction on the right hand side of exclusion condition (4.47) is of the form

$$g(m_P) = \frac{Em_P}{F + Gm_P}$$

where

$$E = \alpha_{RC} e_{RC} K_R$$
$$F = \frac{e_{CP} h_{CP} \alpha_{RP} e_{RP} K_R}{2 e_P h_P}$$
$$G = 1 + \frac{1}{2} e_{RC} h_{RC} K_R - \frac{e_{CP} h_{CP} (1 + e_{RP} h_{RP} K_R)}{e_P h_P}$$

Here, G could be positive or negative. We have that

$$g'(m_P) = \frac{EF}{(F + Gm_P)^2} > 0$$

So, increasing m_P causes the second fraction on the right hand side of exclusion condition (4.47) to increase. But, since we are subtracting the second fraction on the right hand side of the exclusion condition, increasing the second fraction causes the right hand side to decrease.

So, increasing m_P causes the first fraction and second fraction to make the right hand side of exclusion condition (4.47) to decrease, which makes exclusion harder.

In the case where $\frac{1}{2} \alpha_{RP} e_{RP} K_R - m_P (1 + h_{RP} e_{RP} K_R) < 0$, the first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(m_P) = \frac{A}{m_P}$$

where

$$A = \frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_Ph_P\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R\right)}$$

So, increasing m_P causes the first fraction on the right hand side of invasibility condition (4.48) to decrease.

The second fraction on the right hand side of invasibility condition (4.48) is of the form

$$g(m_P) = \frac{Cm_P}{D + Em_P}$$

where

$$C = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$D = \frac{e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}}{e_Ph_P}$$

$$E = 1 + e_{RC}h_{RC}K_R$$

We have that $g'(m_P) > 0$. So, increasing m_P causes the second fraction on the right hand side of invasibility condition (4.48) to increase. But, since we are subtracting the second fraction on the right hand side of the invasibility condition, increasing the second fraction causes the right hand side to decrease.

So, increasing m_P causes both the first fraction and second fraction on the right hand side of invasibility condition (4.48) to result in the right hand side decreasing, which makes invasion easier. □

Before stating the following theorem, we introduce some terminology.

Definition 4.12. *1. We say that increasing e_Ph_P makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of e_Ph_P; i.e., if increasing e_Ph_P reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing e_Ph_P makes it harder for the consumers to invade if the right hand*

side of either invasibility condition (4.46) or (4.48) is an increasing function of e_Ph_P; i.e., if increasing e_Ph_P increases the minimum value of r_C necessary for the consumers to invade.

2. We say that increasing e_Ph_P makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of e_Ph_P; i.e., if increasing e_Ph_P increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing e_Ph_P makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is a decreasing function of e_Ph_P; i.e., if increasing e_Ph_P decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.14. *Increasing e_Ph_P*

1. *makes invasion easier.*

2. *makes exclusion harder if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.*

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, the first fraction on the right hand side of invasibility condition (4.46) is of the form

$$f(e_Ph_P) = \frac{A}{e_Ph_P}$$

where

$$A = \frac{2e_{CP}\alpha_{RP}}{\alpha_{RP} - m_Ph_{RP}}$$

Here, A must be positive because of inequality (4.9). We have

$$f'(e_Ph_P) = -\frac{A}{e_P^2h_P^2} < 0$$

Thus, increasing $e_P h_P$ causes the first fraction on the right hand side of invasibility condition (4.46) to decrease.

The second fraction on the right hand side of invasibility condition (4.46) is of the form

$$g(e_P h_P) = \frac{B e_P h_P}{C + D e_P h_P}$$

where

$$B = \frac{1}{2} \alpha_{RC} e_{RC} K_R$$
$$C = \frac{e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}}{m_P}$$
$$D = 1 + e_{RC} h_{RC} K_R$$

We have that $g'(e_P h_P) > 0$. So, increasing $e_P h_P$ causes the second fraction on the right hand side of invasibility condition (4.46) to increase. But, since we are subtracting the second fraction on the right hand side of invasibility condition (4.46), increasing the second fraction causes the right hand side to decrease.

So, increasing $e_P h_P$ causes both the first fraction and second fraction on the right hand side of invasibility (4.46) to make the right hand side decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.47) is of the form

$$f(e_P h_P) = \frac{A}{e_P h_P}$$

where

$$A = \frac{e_{CP} \left[\frac{1}{2} \alpha_{RP} e_{RP} K_R - m_P (1 + e_{RP} h_{RP} K_R) \right]}{m_P (1 + e_{RP} h_{RP} K_R) + K_R \alpha_{RP} e_{RP}}$$

We have that $f'(e_P h_P) < 0$. Thus, increasing $e_P h_P$ causes the first fraction on the right hand side of exclusion condition (4.47) to decrease.

The second fraction on the right hand side of exclusion condition (4.47) is of the

form

$$g(e_P h_P) = \frac{B e_P h_P}{C + D e_P h_P}$$

where

$$B = \alpha_{RC} e_{RC} K_R$$

$$C = \frac{e_{CP} h_{CP} \left[\frac{1}{2} \alpha_{RP} e_{RP} K_R - m_P (1 + e_{RP} h_{RP} K_R)\right]}{m_P}$$

$$D = 1 + \frac{1}{2} e_{RC} h_{RC} K_R$$

We have that $g'(e_P h_P) > 0$. Thus, increasing $e_P h_P$ causes the second fraction on the right hand side of exclusion condition (4.47) to increase. But, since we are subtracting the second fraction on the right hand side of exclusion condition (4.47), increasing the second fraction causes the right hand side to decrease.

So, increasing $e_P h_P$ causes both the first fraction and second fraction on the right hand side of exclusion condition (4.47) to make the right hand side decrease. This makes exclusion harder.

In the case where $\frac{1}{2} \alpha_{RP} e_{RP} K_R - m_P (1 + h_{RP} e_{RP} K_R) < 0$, the first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(e_P h_P) = \frac{A}{e_P h_P}$$

where

$$A = \frac{e_{CP} K_R \alpha_{RP} e_{RP}}{m_P \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R\right)}$$

We have that $f'(e_P h_P) < 0$. Thus, increasing $e_P h_P$ causes the first fraction on the right hand side of invasibility condition (4.48) to decrease.

The second fraction on the right hand side of invasibility condition (4.48) is of the

form

$$g(e_P h_P) = \frac{B e_P h_P}{C + D e_P h_P}$$

where

$$B = \frac{1}{2} \alpha_{RC} e_{RC} K_R$$

$$C = \frac{e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}}{m_P}$$

$$D = 1 + e_{RC} h_{RC} K_R$$

We have that $g'(e_P h_P) > 0$. Thus, increasing $e_P h_P$ causes the second fraction on the right hand side of invasibility condition (4.48) to increase. But, since we are subtracting the second fraction on the right hand side of invasibility condition (4.48), increasing the second fraction causes the right hand side to decrease.

So, increasing $e_P h_P$ causes both the first fraction and second fraction on the right hand side of invasibility condition (4.48) to make the right hand side decrease. This makes invasion easier. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.13.   *1. We say that increasing h_{RP} makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of h_{RP}; i.e., if increasing h_{RP} reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing h_{RP} makes it harder for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is an increasing function of h_{RP}; i.e., if increasing h_{RP} increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing h_{RP} makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of h_{RP}; i.e., if increasing h_{RP} increases the maximum value of r_C,

below which the consumers will be excluded. We say that increasing h_{RP} makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is a decreasing function of h_{RP}; i.e., if increasing h_{RP} decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.15. *Increasing h_{RP}*

1. *makes invasion easier if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$.*

2. *makes invasion harder if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.*

3. *makes exclusion harder if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.*

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, the second fraction on the right hand side of invasibility condition (4.46) does not depend on h_{RP}, so increasing h_{RP} does not change the consumers' ability to invade the system. The first fraction on the right hand side of invasibility condition (4.46) is of the form

$$f(h_{RP}) = \frac{A}{B - Ch_{RP}}$$

where

$$A = 2e_{CP}\alpha_{RP}$$
$$B = e_P h_P \alpha_{RP}$$
$$C = e_P h_P m_P$$

We have that

$$f'(h_{RP}) = \frac{AC}{(B + Ch_{RP})^2} > 0$$

Thus, increasing h_{RP} causes the right hand side of invasibility condition to (4.46) increase, which makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.47) is of the form

$$f(h_{RP}) = \frac{A - Bh_{RP}}{C + Dh_{RP}}$$

where

$$A = \frac{e_{CP}e_{RP}K_R}{2e_Ph_Pm_P}$$

$$B = \frac{e_{CP}(1 + e_{RP}h_{RP}K_R)}{e_Ph_P}$$

$$C = 1 + e_{RP}h_{RP}K_R$$

$$D = \frac{K_Re_{RP}}{m_P}$$

We have that

$$f'(h_{RP}) = -\frac{BC + AD}{(C + Dh_{RP})^2} < 0$$

Thus, increasing h_{RP} causes the first fraction on the right hand side of exclusion condition (4.47) to decrease.

The second fraction on the right hand side of exclusion condition (4.47) is of the form

$$g(h_{RP}) = \frac{E}{F - Gh_{RP}}$$

where

$$E = \alpha_{RC}e_{RC}K_R$$

$$F = 1 + \frac{1}{2}e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}\left(\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\right)}{e_Ph_Pm_P}$$

$$G = \frac{e_{CP}h_{CP}(1 + e_{RP}h_{RP}K_R)}{e_Ph_P}$$

Here, F could be positive or negative. We have that

$$g'(h_{RP}) = \frac{EG}{(F - Gh_{RP})^2} > 0$$

Thus, increasing h_{RP} causes the second fraction on the right hand side of exclusion condition (4.47) to increase. But since we are subtracting the second fraction on the right hand side of exclusion condition (4.47), increasing the second fraction causes the right hand side to decrease.

So, increasing h_{RP} causes both the first fraction and second fraction on the right hand side of exclusion condition (4.47) to make the right hand side decrease. This makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) < 0$, the second fraction on the right hand side of invasibility condition (4.48) does not depend on h_{RP}, so increasing h_{RP} does not change the consumers' ability to invade. The first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(h_{RP}) = \frac{A}{B + Ch_{RP}}$$

where

$$A = \frac{e_{CP}K_R\alpha_{RP}e_{RP}}{e_P h_P m_P}$$

$$B = 1$$

$$C = \frac{1}{2}e_{RP}K_R$$

Thus, increasing h_{RP} causes the right hand side of invasibility condition (4.48) to decrease, which makes invasion easier. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.14. *1. We say that increasing e_{RP} makes it easier for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is a decreasing function of e_{RP}; i.e., if increasing e_{RP} reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing e_{RP} makes it harder for the consumers to invade if the right hand side of either invasibility condition (4.46) or (4.48) is an increasing function of e_{RP}; i.e., if increasing e_{RP} increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing e_{RP} makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is an increasing function of e_{RP}; i.e., if increasing e_{RP} increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing e_{RP} makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (4.47) or (4.49) is a decreasing function of e_{RP}; i.e., if increasing e_{RP} decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 4.16. *Increasing e_{RP}*

1. makes invasion harder.

2. makes exclusion easier if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$.

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + h_{RP}e_{RP}K_R) > 0$, the first fraction on the right hand side of invasibility condition (4.46) does not depend on e_{RP}, so increasing e_{RP} does not change the consumers' ability to invade the system. The second fraction on the right hand side of invasibility condition (4.46) is of the form

$$f(e_{RP}) = \frac{A}{B + Ce_{RP}}$$

where

$$A = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$B = 1 + e_{RC}h_{RC}K_R$$

$$C = \frac{e_{CP}h_{CP}K_R\alpha_{RP}}{e_P h_P m_P}$$

We have that $f'(e_{RP}) < 0$. Thus, increasing e_{RP} cause the second fraction on the right hand side of invasibility condition (4.46) to decrease. But, since we are subtracting the second fraction on the right hand side of invasibility condition (4.46), decreasing the second fraction causes the right hand side to increase.

So, increasing e_{RP} causes the right hand side of invasibility condition (4.46) to increase, which makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.47) is of the form

$$f(e_{RP}) = \frac{-A + Be_{RP}}{C + De_{RP}}$$

where

$$A = \frac{e_{CP}}{e_P h_P}$$

$$B = \frac{e_{CP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right)}{e_P h_P m_P}$$

$$C = 1$$

$$D = h_{RP}K_R + \frac{K_R\alpha_{RP}}{m_P}e_{CP}$$

Here, B must be positive. To see this, first note that, by assumption, $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1+h_{RP}e_{RP}K_R) > 0$. But, $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1+h_{RP}e_{RP}K_R) > 0 \Leftrightarrow e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right) - m_P > 0$. So we have that $0 < e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right) - m_P < e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right)$. So, $e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right) > 0 \Rightarrow \frac{1}{2}\alpha_{RP} - m_P h_{RP} > 0$.

We have that

$$f'(e_{RP}) = \frac{BC + DA}{(C + De_{RP})^2} > 0$$

So, increasing e_{RP} causes the first fraction on the right hand side of exclusion condition (4.47) to increase.

The second fraction on the right hand side of exclusion condition (4.47) is of the form

$$g(e_{RP}) = \frac{E}{F + Ge_{RP}}$$

where

$$E = \alpha_{RC} e_{RC} K_R$$

$$F = 1 + \frac{1}{2} e_{RC} h_{RC} K_R - \frac{e_{CP} h_{CP}}{e_P h_P}$$

$$G = \frac{e_{CP} h_{CP} K_R \left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right)}{e_P h_P m_P}$$

We have that

$$g'(e_{RP}) = -\frac{EG}{(F + Ge_{RP})^2} < 0$$

Thus, increasing e_{RP} causes the second fraction on the right hand side of exclusion condition (4.47) to decrease. But, since we are subtracting the second fraction on the right hand side of exclusion condition (4.46), decreasing the second fraction causes the right hand side to increase.

So, increasing e_{RP} causes both the first fraction and second fraction to make the right hand side increase, which makes exclusion easier.

In the case where $\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + h_{RP} e_{RP} K_R) < 0$, the first fraction on the right hand side of invasibility condition (4.48) is of the form

$$f(e_{RP}) = \frac{Ae_{RP}}{B + Ce_{RP}}$$

where

$$A = \frac{e_{CP}K_R\alpha_{RP}}{e_P h_P m_P}$$

$$B = 1$$

$$C = \frac{1}{2}h_{RP}K_R$$

Thus, increasing e_{RP} causes the first fraction on the right hand side of invasibility condition (4.48) to increase.

The second fraction on the right hand side of invasibility condition (4.48) is of the form

$$g(e_{RP}) = \frac{D}{E + Fe_{RP}}$$

where

$$D = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$E = 1 + e_{RC}h_{RC}K_R$$

$$F = \frac{e_{CP}h_{CP}K_R\alpha_{RP}}{e_P h_P m_P}$$

Thus, increasing e_{RP} causes the second fraction on the right hand side of invasibility condition (4.48) to decrease. But, since we are subtracting the second fraction on the right hand side of invasibility condition (4.48), decreasing the second fraction causes the right hand side to increase.

So, increasing e_{RP} causes both the first fraction and second fraction on the right hand side of invasibility condition (4.48) to cause the right hand side to increase. This makes invasion harder. $\square$

Boundary Limit Cycle

Now suppose $\alpha_{RP}e_{RP}K_R > m_P(1 + e_{RP}h_{RP}K_R)$, $(e_{RP}h_{RP}K_R - 1)(\alpha_{RP} - m_Ph_{RP}) - 2m_Ph_{RP} > 0$, e_Ph_P sufficiently small, and $\alpha_{RP}e_{RP}K_R$ sufficiently large. Then according to [14], we have the ω-periodic solution $(\psi_R, 0, \psi_P)$, which is stable in the (R, P)-plane. The Floquet multiplier in the C direction is given by

$$\exp\left[\frac{1}{\omega}\int_0^\omega \left(r_C + \frac{\alpha_{RC}\psi_R(t)}{1 + h_{RC}\psi_R(t) + h_{CPP}\psi_P(t)} - \frac{e_{CP}\psi_P(t)}{1 + h_{RP}\psi_R(t) + \psi_P(t)}\right) dt\right].$$

Thus, if (in dimensionalized terms)

$$r_C > \int_0^\omega \left(\frac{e_{CP}\psi_P(t)}{1 + e_{RP}h_{RP}\psi_R(t) + e_Ph_P\psi_P(t)} - \frac{\alpha_{RC}e_{RC}\psi_R(t)}{1 + e_{RC}h_{RC}\psi_R(t) + e_{CP}h_{CP}\psi_P(t)}\right) dt \tag{4.50}$$

then $(\psi_R, 0, \psi_P)$ is unstable in the C direction.

4.8 Invasibility & Exclusion when Predators Absent

Assume we have any of the conditions so that $\left(R^*, C^*\right)$ exists and is stable in the (R, C)-plane. If we linearize the P equation about the equilibrium $\left(R^*, C^*\right)$, we get

$$\frac{dP}{dt} = \left(\frac{\alpha_{RP}R^*}{1 + h_{RP}R^* + h_{PC}C^*} + \frac{\alpha_{CP}C^*}{1 + h_{RP}R^* + h_{CP}C^*} - m_P\right) P. \tag{4.51}$$

In order for the predator to invade the system, we need $\frac{dP}{dt} > 0$, which gives us (in dimensionalized terms)

$$m_P < \frac{\alpha_{RP}e_{RP}R^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{CP}C^*}. \tag{4.52}$$

If we have that

$$m_P > \frac{\alpha_{RP}e_{RP}R^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{CP}C^*}. \tag{4.53}$$

then the predator will be excluded from the system.

There are several possible cases to consider with regards to bounds on R^*. We could have $0 < R < \frac{K_R}{2}$, as could happen in case (1)(a) when there is one interior equilibrium. We could have case (1)(a) when there are three interior equilibria, or case (1)(b) when there are two interior equilibria. We could have $0 < R^* < K_R$, which happens in case (2)(a). We could have $\frac{K_R}{2} < R^* < K_R$, which can happen in case (1)(a) when there is one interior equilibrium, case (1)(a) when there are three interior equilibria, or case (1)(b) when there are two interior equilibria. If $e_{RC} < r_R e_C h_C$, which happens in case (3), we can have $K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) < R^* < K_R$. Note that the parameter dependence of the invasibility and exclusion conditions is the same in the cases where $0 < R^* < \frac{K_R}{2}$ and $0 < R^* < K_R$, so we will only consider the case where $0 < R^* < K_R$. The bounds on C^* will depend on two factors: which case we are in with respect to the bounds on R^* and whether the supersolution to the consumer equation or the consumer isocline's horizontal asymptote give a sharper bound on C^*.

4.8.1 $0 < R^* < K_R$

If $0 < R^* < K_R$ and $e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$ then we use the bounds from on C^* imposed by the supersolution to the consumer equation, given by inequalities (4.25). In this case, invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C \left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C(1 + e_C h_C K_C)}\right)} \tag{4.54}$$

and exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C \left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C(1+e_Ch_CK_C)}\right)}{1 + e_{CP}h_{CP}K_C}. \tag{4.55}$$

If $0 < R^* < K_R$ and $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$ then we use the bounds on C^* imposed by the consumer isocline's horizontal asymptote, given by inequalities (4.25) and (4.26). In this case, invasibility condition (4.52) becomes

$$m_P < \frac{e_{CP}\alpha_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C \left(1 + \frac{\alpha_{RC}}{r_Ch_{RC}}\right)} \tag{4.56}$$

and exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C \left(1 + \frac{\alpha_{RC}}{r_Ch_{RC}}\right)}{1 + e_{CP}h_{CP}K_C}. \tag{4.57}$$

Note that whether the predator is able to invade or is excluded from the system depends in part on parameters which are independent of the predator itself.

Before stating the following theorem, we introduce some terminology.

Definition 4.15. *1. We say that increasing K_C makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of K_C; i.e., if increasing K_C increases the maximum value of m_P, allowed for the predators to invade. We say that increasing K_C makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of K_C; i.e., if increasing K_C reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing K_C makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing

function of K_C; i.e., if increasing K_C decreases the minimum value of m_P which results in the predators being excluded. We say that increasing K_C makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of K_C; i.e., if increasing K_C increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.17. *Increasing K_C*

1. *makes it easier for the predator to invade.*

2. *makes it easier for the predator to be excluded if*

   (a) *$e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $e_Ch_C < \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$, and $K_C > K_C^*$, where K_C is the positive solution to equation (4.60).*

   (b) *$e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $e_Ch_C < \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$, $0 < K_C < K_C^*$, and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$, where K_C is a solution to equation (4.60).*

   (c) *$e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $e_Ch_C > \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$, and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$.*

   (d) *$1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$ and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$.*

3. *makes it harder for the predator to be excluded if*

   (a) *$e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $e_Ch_C < \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$, $0 < K_C < K_C^*$, and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$, where K_C is a solution to equation (4.60).*

   (b) *$e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $e_Ch_C > \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$, and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$*

   (c) *$1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$ and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$.*

Proof. First note that in the case where $e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, we can rewrite invasibility condition (4.54) as

$$m_P < \frac{(1 + e_Ch_CK_C)\alpha_{CP}e_{CP}K_C}{(1 + e_Ch_CK_C)(1 + e_{RP}h_{RP}K_R) + e_{CP}h_{CP}K_C\left(1 + e_Ch_CK_C + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right)} \tag{4.58}$$

and exclusion condition (4.55) as

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C\left(1 + e_Ch_CK_C + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right)}{(1 + e_{CP}h_{CP}K_C)(1 + e_Ch_CK_C)}. \tag{4.59}$$

In this case, the right hand side of invasibility condition (4.58) is of the form

$$f(K_C) = \frac{AK_C + BK_C^2}{C + DK_C + EK_C^2}$$

where

$$A = \alpha_{CP}e_{CP}$$

$$B = \alpha_{CP}e_{CP}e_Ch_C$$

$$C = 1 + e_{RP}h_{RP}K_R$$

$$D = e_Ch_C(1 + e_{RP}h_{RP}K_R) + e_{CP}h_{CP}\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right)$$

$$E = e_Ch_Ce_{CP}h_{CP}$$

We have that
$$f'(K_C) = \frac{(BD - AE)K_C^2 + 2BCK_C + AC}{(C + DK_C + EK_C^2)^2}.$$

Here, $f'(K_C) > 0 \Leftrightarrow (BD - AE)K_C^2 + 2BCK_C + AC > 0$ and $f'(K_C) < 0 \Leftrightarrow (BD - AE)K_C^2 + 2BCK_C + AC < 0$. Let $q(K_C) = (BD - AE)K_C^2 + 2BCK_C + AC$. The vertex of q is located at $K_C = -\frac{BC}{BD - AE}$ and the y-intercept is located at $q = AC > 0$. If $BD - AE > 0$, then the graph of q opens upward, the vertex is to the left of the

q-axis, and the q-intercept is positive. In this case, $f'(K_C) > 0$ for all biologically relevant values of K_C. But, if $BD - AE < 0$, then the graph of q opens downward, the vertex is to the right of the q-axis, and the q-intercept is positive. In this case, $f'(K_C) > 0$ for $0 < K_C < K_C^*$ and $f'(K_C) < 0$ for $K_C > K_C^*$, where K_C^* is the positive solution to the equation $(BD - AE)K_C^2 + 2BCK_C + AC = 0$. Note that

$$BD - AE > 0 \Leftrightarrow \alpha_{CP} e_{CP} e_C h_C \left[e_C h_C (1 + e_{RP} h_{RP} K_R) + e_{CP} h_{CP} \left(1 + \frac{\alpha_{RC} e_{RC} K_R}{r_C} \right) \right]$$

$$- \alpha_{CP} e_{CP} e_C h_C e_{CP} h_{CP}$$

$$\Leftrightarrow e_C h_C (1 + e_{RP} h_{RP} K_R) + e_{CP} h_{CP} \left(1 + \frac{\alpha_{RC} e_{RC} K_R}{r_C} \right) - e_{CP} h_{CP}$$

$$\Leftrightarrow e_C h_C (1 + e_{RP} h_{RP} K_R) + \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C} > 0$$

and

$$BD - AE < 0 \Leftrightarrow e_C h_C (1 + e_{RP} h_{RP} K_R) + \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C} < 0.$$

So, for all biologically relevant values of the parameters, we must have $f'(K_C) > 0$. Thus, increasing K_C causes the right hand side of invasibility condition (4.58) to increase. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.59) is of the form

$$f(K_C) = \frac{A}{B + CK_C}$$

where

$$A = \alpha_{RP} e_{RP} K_R$$

$$B = 1$$

$$C = e_{CP} h_{PC}$$

We have that $f'(K_C) < 0$, so increasing K_C causes the first fraction on the right hand side of exclusion condition (4.59) to decrease.

The second fraction on the right hand side of exclusion condition (4.59) is of the form

$$g(K_C) = \frac{DK_C + EK_C^2}{F + GK_C + HK_C^2}$$

where

$$D = \alpha_{CP}e_{CP}\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right)$$

$$E = \alpha_{CP}e_{CP}e_Ch_C$$

$$F = 1$$

$$G = e_{CP}h_{CP} + e_Ch_C$$

$$H = e_{CP}h_{CP}e_Ch_C$$

If $EG - DH > 0$ then $g'(K_C) > 0$ for all biologically relevant values of K_C. But if $EG - DH < 0$ then we will have $g'(K_C) > 0$ for $0 < K_C < K_C^*$ and $g'(K_C) < 0$ for $K_C > K_C^*$, where K_C^* is the positive solution to the equation

$$(EG - DH)K_C^2 + 2EFK_C + DF = 0. \tag{4.60}$$

Note that

$$EG - DH > 0 \Leftrightarrow \alpha_{CP}e_{CP}e_Ch_C(e_{CP}h_{CP} + e_Ch_C)$$
$$- \alpha_{CP}e_{CP}^2h_{CP}e_Ch_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right) > 0$$
$$\Leftrightarrow (e_{CP}h_{CP} + e_Ch_C) - e_{CP}h_{CP}\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C}\right) > 0$$
$$\Leftrightarrow e_Ch_C > \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}K_R}{r_C}$$

and

$$EG - DH < 0 \Leftrightarrow e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}.$$

So, if $e_C h_C > \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ then the right hand side of exclusion condition (4.59) is increasing. But if $e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ then the right hand side of exclusion condition (4.59) is increasing when $0 < K_C < K_C^*$ and decreasing when $K_C > K_C^*$.

Thus, when $e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ and $K_C > K_C^*$, increasing K_C causes both the first and second fractions on the right hand side of exclusion condition (4.59) to decrease. When we add these fractions together, we have that the right hand side of exclusion condition (4.59) is decreasing, which makes exclusion easier. But when $e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ with $0 < K_C < K_C^*$ or when $e_C h_C > \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ then increasing K_C causes the first fraction on the right hand side of exclusion condition (4.59) to decrease while causing the second fraction to increase. When we add these fractions together, we get that the right hand side of exclusion condition (4.59) could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side dominates the second fraction, so increasing K_C causes the right hand side to decrease. This makes exclusion easier. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side dominates the first fraction, so increasing K_C causes the right hand side to increase. This makes exclusion harder.

In the case where $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$, the right hand side of invasibility condition (4.56) is of the form

$$f(K_C) = \frac{A K_C}{B + C K_C}$$

where

$$A = e_{CP}\alpha_{CP}$$

$$B = 1 + e_{RP}h_{RP}K_R$$

$$C = e_{CP}h_{CP}\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

We have that $f'(K_C) > 0$ so increasing K_C causes the right hand side of invasibility condition (4.56) to increase. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.57) is of the form

$$f(K_C) = \frac{A}{B + CK_C}$$

where

$$A = \alpha_{RP}e_{RP}K_R$$

$$B = 1$$

$$C = e_{CP}h_{PC}$$

We have that $f'(K_C) < 0$, so increasing K_C causes the first fraction on the right hand side of exclusion condition (4.57) to decrease.

The second fraction on the right hand side of exclusion condition (4.57) is of the form

$$g(K_C) = \frac{DK_C}{E + FK_C}$$

where

$$D = \alpha_{CP} e_{CP} \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}} \right)$$

$$E = 1$$

$$F = e_{CP} h_{CP}$$

We have that $g'(K_C) > 0$, so increasing K_C causes the second fraction on the right hand side of exclusion condition (4.57) to increase.

Thus, increasing K_C causes the first fraction on the right hand side of exclusion condition (4.57) to decrease while causing the second fraction to increase. When we add these fractions together, we get that the right hand side of exclusion condition (4.57) could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side will dominate the second fraction. So, increasing K_C will cause the right hand side of exclusion condition (4.57) to decrease, which makes exclusion easier. But, if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side will dominate the first fraction. So, increasing K_C will cause the right hand side of exclusion condition (4.57) to increase, which makes exclusion harder. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.16. *1. We say that increasing K_R makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of K_R; i.e., if increasing K_R increases the maximum value of m_P, allowed for the predators to invade. We say that increasing K_R makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of K_R; i.e., if increasing K_R reduces the maximum value of m_P allowed for the predators to invade.*

2. *We say that increasing K_R makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of K_R; i.e., if increasing K_R decreases the minimum value of m_P which results in the predators being excluded. We say that increasing K_R makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of K_R; i.e., if increasing K_R increases the minimum value of m_P which results in the predators being excluded.*

Theorem 4.18. *Increasing K_R*

1. *makes it harder for the predator to invade.*

2. *makes it harder for the predator to be excluded.*

Proof. In the case where $e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the right hand side of invasibility condition (4.54) is of the form

$$f(K_R) = \frac{A}{B + CK_R}$$

where

$$A = \alpha_{CP}e_{CP}K_C$$
$$B = 1 + e_{CP}h_{CP}K_C$$
$$C = e_{RP}h_{RP} + \frac{e_{CP}h_{CP}\alpha_{RC}e_{RC}}{r_C(1 + e_C h_C K_C)}$$

We have that $f'(K_R) < 0$ so increasing K_R causes the right hand side of invasibility condition (4.54) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.55) is of the form

$$f(K_R) = AK_R$$

where

$$A = \frac{\alpha_{RP} e_{RP}}{1 + e_{CP} h_{PC} K_C}$$

We have that $f'(K_R) > 0$ so increasing K_R causes the first fraction on the right hand side of exclusion condition (4.55) to increase.

The second fraction on the right hand side of exclusion condition (4.55) is of the form

$$g(K_R) = B + CK_R$$

where

$$B = \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$$

$$C = \frac{\alpha_{CP} e_{CP} K_C \alpha_{RC} e_{RC}}{r_C (1 + e_C h_C K_C)(1 + e_{CP} h_{CP} K_C)}$$

We have that $g'(K_R) > 0$ so increasing K_R causes the second fraction on the right hand side of exclusion condition (4.55) to increase.

Thus, increasing K_R causes both the first and second fraction on the right hand side of exclusion condition (4.55) to increase. This causes the right hand side of the exclusion condition to increase, which makes exclusion harder.

In the case where $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$, the right hand side of invasibility condition (4.56) is of the form

$$f(K_R) = \frac{A}{B + CK_R}$$

where

$$A = e_{CP}\alpha_{CP}K_C$$

$$B = 1 + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

$$C = e_{RP}h_{RP}$$

We have that $f'(K_R) < 0$ so increasing K_R causes the right hand side of invasibility condition (4.56) to decrease, which makes invasion harder.

The second fraction on the right hand side of exclusion condition (4.57) is independent of K_R. The first fraction on the right hand side of exclusion condition (4.57) is of the form

$$f(K_R) = AK_R$$

where

$$A = \frac{\alpha_{RP}e_{RP}}{1 + e_{CP}h_{PC}K_C}$$

We have that $f'(K_R) > 0$ so increasing K_R the right hand side of exclusion condition (4.57) to increase. This makes exclusion harder. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.17. *1. We say that increasing α_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of α_{RC}; i.e., if increasing α_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing α_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of α_{RC}; i.e., if increasing α_{RC} reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing α_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of α_{RC}; i.e., if increasing α_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing α_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of α_{RC}; i.e., if increasing α_{RC} increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.19. *Increasing α_{RC}*

1. *makes it harder for the predator to invade.*

2. *makes it easier for the predator to be excluded.*

Proof. In the case where $e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, the right hand side of invasibility condition (4.54) is of the form

$$f(\alpha_{RC}) = \frac{A}{B + C\alpha_{RC}}$$

where

$$A = \alpha_{CP}e_{CP}K_C$$

$$B = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C$$

$$C = \frac{\alpha_{CP}e_{CP}K_Ce_{RC}K_R}{r_C(1 + e_Ch_CK_C)}$$

We have that $f'(\alpha_{RC}) < 0$ so increasing α_{RC} causes the right hand side of invasibility condition (4.54) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.55) is independent of α_{RC}. The second fraction on the right hand side of exclusion condition (4.55)

is of the form

$$f(\alpha_{RC}) = A + B\alpha_{RC}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C e_{RC}K_R}{r_C(1 + e_C h_C K_C)(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(\alpha_{RC}) > 0$. So increasing α_{RC} causes the right hand side of exclusion condition (4.55) to increase, which makes exclusion easier.

In the case where $1 + e_C h_C K_C < e_{RC}h_{RC}K_R$, the right hand side of invasibility condition (4.56) is of the form

$$f(\alpha_{RC}) = \frac{A}{B + C\alpha_{RC}}$$

where

$$A = e_{CP}\alpha_{CP}K_C$$

$$B = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C$$

$$C = \frac{e_{CP}h_{CP}K_C}{r_C h_{RC}}$$

We have that $f'(\alpha_{RC}) < 0$ so increasing α_{RC} causes the right hand side of invasibility condition (4.56) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.57) is independent of α_{RC}. The second fraction on the right hand side of exclusion condition (4.57) is of the form

$$f(\alpha_{RC}) = A + B\alpha_{RC}$$

where

$$A = \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$$

$$B = \frac{\alpha_{CP} e_{CP} K_C}{r_C h_{RC}(1 + e_{CP} h_{CP} K_C)}$$

We have that $f'(\alpha_{RC}) > 0$ so increasing α_{RC} causes the right hand side of exclusion condition (4.57) to increase. This makes exclusion easier. $\qquad\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.18. *1. We say that increasing e_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of e_{RC}; i.e., if increasing e_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing e_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of e_{RC}; i.e., if increasing e_{RC} reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing e_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of e_{RC}; i.e., if increasing e_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing e_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of e_{RC}; i.e., if increasing e_{RC} increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.20. *Increasing e_{RC}*

1. makes it harder for the predator to invade.

2. makes it harder for the predator to be excluded.

Proof. In the case where $e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the right hand side of invasibility condition (4.54) is of the form

$$f(e_{RC}) = \frac{A}{B + Ce_{RC}}$$

where

$$A = \alpha_{CP}e_{CP}K_C$$

$$B = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C$$

$$C = \frac{e_{CP}h_{CP}K_C\alpha_{RC}K_R}{r_C(1 + e_C h_C K_C)}$$

We have that $f'(e_{RC}) < 0$ so increasing e_{RC} causes the right hand side of invasibility condition (4.54) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.55) is independent of e_{RC}. The second fraction on the right hand side of exclusion condition (4.55) is of the form

$$f(e_{RC}) = A + Be_{RC}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}K_C}{r_C(1 + e_C h_C K_C)(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(e_{RC}) > 0$ so increasing e_{RC} causes the right hand side of exclusion condition (4.55) to increase. This makes exclusion harder.

In the case where $1 + e_C h_C K_C < e_{RC}h_{RC}K_R$, the right hand side of both invasibility condition (4.56) and exclusion condition (4.57) are independent of e_{RC}. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.19. *1. We say that increasing $e_C h_C$ makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ increases the maximum value of m_P, allowed for the predators to invade. We say that increasing $e_C h_C$ makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing $e_C h_C$ makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ decreases the minimum value of m_P which results in the predators being excluded. We say that increasing $e_C h_C$ makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.21. *Increasing $e_C h_C$*

(a) makes it easier for the predator to invade if $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$.

(b) makes it easier for the predator to be excluded if $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$.

(c) has no effect on whether the predator can invade or is excluded, if $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$.

Proof. First note that in the case where $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$, we can rewrite

invasibility condition (4.54) as

$$m_P < \frac{r_C(1 + e_C h_C K_C)\alpha_{CP} e_{CP} K_C}{r_C(1 + e_C h_C K_C)(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C) + e_{CP} h_{CP} K_C \alpha_{RC} e_{RC} K_R}$$

(4.61)

and exclusion condition (4.55) as

$$m_P > \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{CP} h_{PC} K_C} + \frac{\alpha_{CP} e_{CP} K_C (1 + e_C h_C K_C) + \frac{\alpha_{RC} e_{RC} K_R \alpha_{CP} e_{CP} K_C}{r_C}}{(1 + e_{CP} h_{CP} K_C)(1 + e_C h_C K_C)}.$$

(4.62)

The right hand side of invasibility condition (4.61) is of the form

$$f(e_C h_C) = \frac{A + B e_C h_C}{C + D e_C h_C}$$

where

$$A = r_C \alpha_{CP} e_{CP} K_C$$

$$B = r_C \alpha_{CP} e_{CP} K_C^2$$

$$C = r_C(1 + e_{PR} h_{RP} K_R + e_{CP} h_{CP} K_C) + e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R$$

$$D = r_C K_C(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

We have that

$$f'(e_C h_C) = \frac{BC - AD}{(C + D e_C h_C)^2} \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}.$$

Note that

$$BC > AD \Leftrightarrow \alpha_{CP}e_{CP}K_C^2 r_C \left[r_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R \right]$$

$$> r_C^2\alpha_{CP}e_{CP}K_C^2(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

$$\Leftrightarrow r_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R$$

$$> r_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

$$\Leftrightarrow e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R > 0$$

and

$$BC < AD \Leftrightarrow e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R < 0$$

So for all biologically relevant values of the parameters, we have that $f'(e_Ch_C) > 0$. Therefore, increasing e_Ch_C causes the right hand side of invasibility condition (4.61) to increase, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.62) is independent of e_Ch_C. The second fraction on the right hand side of exclusion condition (4.62) is of the form

$$f(e_Ch_C) = \frac{A + Be_Ch_C}{C + De_Ch_C}$$

where

$$A = \alpha_{CP}e_{CP}K_C + \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}e_{RC}K_R}{r_C}$$

$$B = \alpha_{CP}e_{CP}K_C^2$$

$$C = 1 + e_{CP}h_{CP}K_C$$

$$D = K_C(1 + e_{CP}h_{CP}K_C)$$

We have that $f'(e_C h_C) > 0$ if $BC > AD$ and $f'(e_C h_C) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \alpha_{CP} e_{CP} K_C^2 (1 + e_{CP} h_{CP} K_C)$$
$$> K_C (1 + e_{CP} h_{CP} K_C) \left(\alpha_{CP} e_{CP} K_C + \frac{\alpha_{CP} e_{CP} K_C \alpha_{RC} e_{RC} K_R}{r_C} \right)$$
$$\Leftrightarrow \alpha_{CP} e_{CP} K_C > \alpha_{CP} e_{CP} K_C \left(1 + \frac{\alpha_{RC} e_{RC} K_R}{r_C} \right)$$
$$\Leftrightarrow 0 > \frac{\alpha_{RC} e_{RC} K_R}{r_C}$$

and

$$BC < AD \Leftrightarrow 0 < \frac{\alpha_{RC} e_{RC} K_R}{r_C}$$

So for all biologically relevant values of the parameters, we have that $f'(e_C h_C) < 0$. Thus, increasing $e_C h_C$ causes the right hand side of exclusion condition (4.62) to decrease, which exclusion easier.

In the case where $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$, the right hand side of both invasibility condition (4.56) and exclusion condition (4.57) are independent of $e_C h_C$, so increasing $e_C h_C$ does not change whether the predator can invade or is excluded. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.20. *1. We say that increasing r_C makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of r_C; i.e., if increasing r_C increases the maximum value of m_P, allowed for the predators to invade. We say that increasing r_C makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of r_C; i.e., if increasing r_C reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing r_C makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing

function of r_C; i.e., if increasing r_C decreases the minimum value of m_P which results in the predators being excluded. We say that increasing r_C makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of r_C; i.e., if increasing r_C increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.22. *Increasing r_C*

(a) makes it easier for the predator to invade.

(b) makes it easier for the predator to be excluded.

Proof. In the case where $e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, we can rewrite invasibility condition (4.54) as

$$m_P < \frac{\alpha_{CP} e_{CP} K_C r_C}{r_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + \frac{e_{CP}h_{CP}K_C \alpha_{RC} e_{RC} K_R}{1 + e_C h_C K_C}}. \tag{4.63}$$

The right hand side of invasibility condition (4.63) is of the form

$$f(r_C) = \frac{A r_C}{B + C r_C}$$

where

$$A = \alpha_{CP} e_{CP} K_C$$
$$B = \frac{e_{CP} h_{CP} K_C \alpha_{RC} e_{RC} K_R}{1 + e_C h_C K_C}$$
$$C = 1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C$$

We have that $f'(r_C) > 0$ so increasing r_C causes the right hand side of invasibility condition (4.63) to increase. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.55) is independent of r_C. The second fraction on the right hand side of exclusion condition (4.55) is of the form

$$f(r_C) = A + \frac{B}{r_C}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}e_{RC}K_R}{(1 + e_Ch_CK_C)(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(r_C) < 0$ so increasing r_C causes the right hand side of exclusion condition (4.55) to decrease. This makes exclusion easier.

In the case where $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$, we can rewrite invasibility condition (4.56) as

$$m_P < \frac{e_{CP}\alpha_{CP}K_Cr_C}{r_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + \frac{e_{CP}h_{CP}K_C\alpha_{RC}}{h_{RC}}}. \tag{4.64}$$

The right hand side of invasibility condition (4.64) is of the form

$$f(r_C) = \frac{Ar_C}{B + Cr_C}$$

where

$$A = e_{CP}\alpha_{CP}K_C$$

$$B = \frac{e_{CP}h_{CP}K_C\alpha_{RC}}{h_{RC}}$$

$$C = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C$$

We have that $f'(r_C) > 0$ so increasing r_C causes the right hand side of invasibility condition (4.64) to increase. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.57) is indepen-

dent of r_C. The second fraction on the right hand side of exclusion condition (4.57) is of the form

$$f(r_C) = A + \frac{B}{r_C}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}}{h_{RC}(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(r_C) < 0$ so increasing r_C causes the right hand side of exclusion condition (4.57) to decrease. This makes exclusion easier. $\qquad\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.21. *1. We say that increasing h_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of h_{RC}; i.e., if increasing h_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing h_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of h_{RC}; i.e., if increasing h_{RC} reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing h_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of h_{RC}; i.e., if increasing h_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing h_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of h_{RC}; i.e., if increasing h_{RC} increases the minimum value of m_P which results in the predators being

excluded.

Theorem 4.23. *Increasing h_{RC}*

(a) makes it easier for the predator to invade if $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$.

(b) makes it easier for the predator to be excluded if $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$.

(c) has no effect on whether the predator can invade or is excluded if $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$.

Proof. In the case where $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$, the right hand side of both invasibility condition (4.54) and exclusion condition (4.55) are independent of h_{RC}. So increasing h_{RC} does not change whether or not the predator can invade or is excluded from the system.

In the case where $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$, the right hand side of invasibility condition (4.56) is of the form

$$f(h_{RC}) = \frac{A h_{RC}}{B + C h_{RC}}$$

where

$$A = e_{CP} \alpha_{CP} K_C$$
$$B = \frac{e_{CP} \alpha_{CP} K_C \alpha_{RC}}{r_C}$$
$$C = 1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C$$

We have that $f'(h_{RC}) > 0$ so increasing h_{RC} causes the right hand side of invasibility condition (4.56) to increase. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.57) is independent of h_{RC}. The second fraction on the right hand side of exclusion condition (4.57)

is of the form

$$f(h_{RC}) = A + \frac{B}{h_{RC}}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}}{r_C(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(h_{RC}) < 0$. So, increasing h_{RC} causes the right hand side of exclusion condition (4.57) to decrease, which makes exclusion easier. $\qquad\square$

4.8.2 $\quad \frac{K_R}{2} < R^* < K_R$

If $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$ then we use the bounds on C^* imposed by the supersolution to the consumer equation, given by inequalities (4.27) . In this case, invasibility condition (4.52) becomes

$$m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}K_R+e_Ch_CK_C\right)}\right)} \tag{4.65}$$

$$+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}K_R+e_Ch_CK_C\right)}\right)} \tag{4.66}$$

and exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}K_R+e_Ch_CK_C\right)}\right)}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C}.$$

$$\tag{4.67}$$

We can rewrite invasibility condition (4.65) as

$$m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}{r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)\left(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\right) + e_{CP}h_{PC}K_C\alpha_{RC}e_{RC}K_R}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}{r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)\left(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right) + e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R}$$

(4.68)

and exclusion condition (4.67) as

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right) + \alpha_{CP}e_{CP}K_C\alpha_{RC}e_{RC}K_R}{\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}$$

(4.69)

If $\frac{K_R}{2} < R^* < K_R$ and $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$ then we use the bounds on C^* imposed by the consumer isocline's horizontal asymptote, given by (4.28). In this case, invasibility condition (4.52) becomes

$$m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}$$

(4.70)

and exclusion condition (4.67) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}{1 + e_{CP}h_{CP}K_C}.$$

(4.71)

We can rewrite invasibility condition (4.70) as

$$m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R r_C h_{RC}}{r_C h_{RC}(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C r_C h_{RC}}{r_C h_{RC}(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + e_{CP}h_{CP}K_C\alpha_{RC}}$$

(4.72)

and exclusion condition (4.71) as

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C} + \frac{r_C h_{RC}\alpha_{CP}e_{CP}K_C + \alpha_{CP}e_{CP}K_C\alpha_{RC}}{r_C h_{RC}(1 + e_{CP}h_{CP}K_C)}. \quad (4.73)$$

Note that whether the predator is able to invade or is excluded from the system depends in part on parameters which are independent of the predator itself.

Before stating the following theorem, we introduce some terminology.

Definition 4.22.   *1. We say that increasing K_C makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of K_C; i.e., if increasing K_C increases the maximum value of m_P, allowed for the predators to invade. We say that increasing K_C makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of K_C; i.e., if increasing K_C reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing K_C makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of K_C; i.e., if increasing K_C decreases the minimum value of m_P which results in the predators being excluded. We say that increasing K_C makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of α_{RC}; i.e., if increasing K_C increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.24. *If $\frac{K_R}{2} < R^* < K_R$, then increasing K_C*

1. makes it easier for the predator to invade if $\alpha_{RP}e_{RP} \ll \alpha_{CP}e_{CP}$.

2. makes it harder for the predator to invade if $\alpha_{RP}e_{RP} \gg \alpha_{CP}e_{CP}$.

3. *makes it easier for the predator to be excluded if* $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$.

4. *makes it harder for the predator to be excluded if* $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$.

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(K_C) = \frac{A + BK_C}{C + DK_C + EK_C^2}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$B = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C e_C h_C$$

$$C = r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R)$$

$$D = r_C \left[e_{CP}h_{PC}\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right) + e_C h_C (1 + e_{RP}h_{RP}K_R)\right] + e_{CP}h_{PC}\alpha_{RC}e_{RC}K_R$$

$$E = e_C h_C e_{CP} h_{PC}$$

We have that

$$f'(K_C) = -\frac{BEK_C^2 + 2AEK_C + (DA - BC)}{(C + DK_C + EK_C^2)^2}$$

$$\begin{cases} > 0 \text{ if } -BEK_C^2 - 2AEK_C + (BC - AD) > 0 \\ < 0 \text{ if } -BEK_C^2 - 2AEK_C + (BC - AD) < 0 \end{cases}.$$

The vertex of the quadratic function $q(K_C) = -BEK_C^2 - 2AEK_C + (BC - AD)$ is $K_C = -\frac{A}{B} < 0$. The q-intercept is

$$q = BC - DA \begin{cases} > 0 \text{ if } BC > DA \\ < 0 \text{ if } BC < DA \end{cases}$$

If $BC < DA$ then the graph of q opens downward, the vertex is to the left of the q-axis and the q-intercept is below the K_C-axis, so we have $f'(K_C) < 0$. But, if $BC > DA$ then the graph of q opens downward, the vertex is to the left of the q-axis, and the q-intercept is above the K_C-axis, so we have $f'(K_C) > 0$ for $0 < K_C < K_C^*$ and $f'(K_C) < 0$ for $K_C > K_C^*$, where K_C^* is the positive root of the equation $-BEK_C^2 - 2AEK_C + (BC - AD) = 0$. Note that

$$BC > DA \Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C^2 e_C h_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R)$$

$$> \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$\left[r_C\left(\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)e_{CP}h_{PC} + e_C h_C(1 + e_{RP}h_{RP}K_R)\right) + e_{CP}h_{PC}\alpha_{RC}e_{RC}K_R\right]$$

$$\Leftrightarrow r_C e_C h_C(1 + e_{RP}h_{RP}K_R)$$

$$> r_C \left[\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)e_{CP}h_{PC} + e_C h_C(1 + e_{RP}h_{RP}K_R)\right] + e_{CP}h_{PC}\alpha_{RC}e_{RC}K_R$$

$$\Leftrightarrow 0 > r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right) + e_{CP}h_{PC}\alpha_{RC}e_{RC}K_R$$

and

$$BC < DA \Leftrightarrow 0 < r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right) + e_{CP}h_{PC}\alpha_{RC}e_{RC}K_R.$$

So, for all biologically relevant values of the parameters, we must have $f'(K_C) < 0$. Thus, increasing K_C causes the first fraction on the right hand side of invasibility condition (4.68) to decrease.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$g(K_C) = \frac{AK_C + BK_C^2}{C + DK_C + EK_C^2}$$

where

$$A = \alpha_{CP} e_{CP} r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)$$

$$B = \alpha_{CP} e_{CP} r_C e_C h_C$$

$$C = r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)(1 + e_{RP} h_{RP} K_R)$$

$$D = r_C \left[\left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) e_{CP} h_{CP} + (1 + e_{RP} h_{RP} K_R) e_C h_C\right] + e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R$$

$$E = r_C e_C h_C e_{CP} h_{CP}$$

We have that

$$g'(K_C) = \frac{(BD - AE)K_C^2 + 2BCK_C + AC}{\left(C + DK_C + EK_C^2\right)^2} \begin{cases} > 0 \text{ if } (BD - AE)K_C^2 + 2BCK_C + AC > 0 \\ \\ < 0 \text{ if } (BD - AE)K_C^2 + 2BCK_C + AC < 0 \end{cases}$$

The q-intercept of the quadratic function $q(K_C) = (BD - AE)K_C^2 + 2BCK_C + AC$

is $q = AC > 0$. The vertex is at

$$K_C = -\frac{BC}{BD - AE} \begin{cases} > 0 \text{ if } BD < AE \\ \\ < 0 \text{ if } BD > AE \end{cases}.$$

So, if $BD > AE$ then q opens upward, the q-intercept is above the K_C-axis, and the vertex is to the right of the q-axis. In this case, $g'(K_C) > 0$. But if $BD < AE$ then q opens downward, the q-intercept is above the K_C-axis, and the vertex is to the right of the q-axis. In this case, $g'(K_C) > 0$ if $0 < K_C < K_C^*$ and $g'(K_C) < 0$ if $K_C > K_C^*$, where K_C^* is the positive root of the equation $(BD - AE)K_C^2 + 2BCK_C + AC = 0$.

Note that

$$BD > AE \Leftrightarrow \alpha_{CP}e_{CP}r_Ce_Ch_C\left(r_C\left[\left(1+\frac{1}{2}e_{RC}h_{RC}K_R\right)e_{CP}h_{CP}+(1+e_{RP}h_{RP}K_R)e_Ch_C\right]\right)$$

$$+\alpha_{CP}e_{CP}r_Ce_Ch_Ce_{CP}h_{CP}\alpha_{RC}e_{RC}K_R > r_C^2e_Ch_Ce_{CP}h_{CP}\alpha_{CP}e_{CP}\left(1+\frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$\Leftrightarrow r_C^2\left[\left(1+\frac{1}{2}e_{RC}h_{RC}K_R\right)e_{CP}h_{CP}+(1+e_{RP}h_{RP}K_R)e_Ch_C\right]+r_Ce_{CP}h_{CP}\alpha_{RC}e_{RC}K_R$$

$$> r_C^2h_{CP}e_{CP}\left(1+\frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$\Leftrightarrow r_C^2e_Ch_C(1+e_{RP}h_{RP}K_R)+r_Ce_{CP}h_{CP}\alpha_{RC}e_{RC}K_R > 0$$

and

$$BD < AE \Leftrightarrow r_C^2e_Ch_C(1+e_{RP}h_{RP}K_R)+r_Ce_{CP}h_{CP}\alpha_{RC}e_{RC}K_R < 0.$$

So for any biologically relevant values of the parameters, we must have $g'(K_C) > 0$. Thus, increasing K_C causes the second fraction on the right hand side of invasibility condition (4.68) to increase.

So, increasing K_C causes the first fraction on the right hand side of invasibility condition (4.68) to decrease, while causing the second fraction to increase. Thus, when we add these fraction together, we get that the right hand side of invasibility condition (4.68) could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then the first fraction on the right hand side of invasibility condition (4.68) will dominate the second fraction. In this case, increasing K_C causes the right hand side of invasibility condition (4.68) to decrease, which makes invasion harder. But if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then the second fraction on the right hand side of invasibility condition (4.68) dominates the first fraction. In this case, increasing K_C causes the right hand side of invasibility condition (4.68) to increase, which makes invasion easier.

The first fraction on the right hand side of (4.69) exclusion condition is of the

form

$$f(K_C) = \frac{A}{B + CK_C}$$

where

$$A = \alpha_{RP} e_{RP} K_R$$

$$B = 1 + \frac{1}{2} e_{RP} h_{RP} K_R$$

$$C = e_{CP} h_{PC} K_C$$

We have that $f'(K_C) < 0$ so increasing K_C causes the first fraction on the right hand side of exclusion condition (4.69) to decrease.

The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$g(K_C) = \frac{AK_C + BK_C^2}{C + DK_C + EK_C^2}$$

where

$$A = \alpha_{CP} e_{CP} r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) + \alpha_{CP} e_{CP} \alpha_{RC} e_{RC} K_R$$

$$B = \alpha_{CP} e_{CP} r_C e_C h_C$$

$$C = \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R\right)\left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)$$

$$D = e_C h_C \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R\right) + e_{CP} h_{CP} \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)$$

$$E = e_{CP} h_{CP} e_C h_C$$

We have that $g'(K_C) > 0$ if $(BD - AE)K_C^2 + 2BCK_C + AC > 0$ and $g'(K_C) < 0$ if $(BD - AE)K_C^2 + 2BCK_C + AC < 0$. The q-intercept of the quadratic function

$q(K_C) = (BD - AE)K_C^2 + 2BCK_C + AC$ is $q = AC > 0$. The vertex is located at

$$K_C = -\frac{BC}{BD - AE} \begin{cases} > 0 \text{ if } BD < AE \\ \\ < 0 \text{ if } BD > AE \end{cases}.$$

If $BD > AE$ then $g'(K_C) > 0$. If $BD < AE$ then $g'(K_C) > 0$ for $0 < K_C < K_C^*$ and $g'(K_C) < 0$ for $K_C > K_C^*$, where K_C^* is the positive root of $q(K_C) = 0$. Note that

$$BD > AE \Leftrightarrow \alpha_{CP}e_{CP}r_Ce_Ch_C \left[e_Ch_C \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R \right) + e_{CP}h_{CP} \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R \right) \right]$$

$$> \alpha_{CP}e_{CP}e_Ce_{CP}h_{CP}e_Ch_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R \right)$$

$$\Leftrightarrow e_Ch_C \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R \right) + e_{CP}h_{CP} \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R \right)$$

$$> e_{CP}h_{CP} \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R \right)$$

$$\Leftrightarrow e_Ch_C \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R \right) < 0$$

and

$$BD < AE \Leftrightarrow e_Ch_C \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R \right) < 0.$$

So, for all biologically relevant values of the parameters, we have that $g'(K_C) > 0$. Thus, increasing K_C causes the second fraction on the right hand side of exclusion condition (4.69) to increase.

So, increasing K_C causes the first fraction on the right hand side of exclusion condition (4.69) to decrease, while causing the second fraction to increase. Thus, when we add these fractions together, we have that the right hand side of the exclusion condition could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then the first fraction on the right hand side of exclusion condition (4.69) dominates the second fraction. In this case, increasing K_C causes the right hand side of exclusion condition (4.69) to decrease. This makes exclusion easier. But if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then the second fraction on the right hand side of exclusion

condition (4.69) dominates the first fraction. In this case, increasing K_C causes the right hand side of exclusion condition (4.69) to increase. This makes exclusion harder.

In the case where $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$, the first fraction on the right hand side of invasibility condition (4.72) is of the form

$$f(K_C) = \frac{A}{B + CK_C}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C h_{RC}$$

$$B = r_C h_{RC}(1 + e_{RP}h_{RP}K_R)$$

$$C = r_C h_{RC}e_{CP}h_{PC} + e_{CP}h_{PC}\alpha_{RC}$$

We have that $f'(K_C) < 0$, so increasing K_C causes the first fraction on the right hand side of invasibility condition (4.72) to decrease.

The second fraction on the right hand side of invasibility condition (4.72) is of the form

$$g(K_C) = \frac{DK_C}{E + FK_C}$$

where

$$D = \alpha_{CP}e_{CP}r_C h_{RC}$$

$$E = r_C h_{RC}(1 + e_{RP}h_{RP}K_R)$$

$$F = r_C h_{RC}e_{CP}h_{CP} + e_{CP}h_{CP}\alpha_{RC}$$

We have that $g'(K_C) > 0$, so increasing K_C causes the second fraction on the right hand side of invasibility condition (4.72) to increase.

So, increasing K_C causes the first fraction on the right hand side of invasibility

condition (4.72) to decrease, while causing the second fraction to increase. Thus, when we add these fraction together, we get that the right hand side of the invasibility condition could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side of invasibility condition (4.72) dominates the second fraction. In this case, increasing K_C causes the right hand side of invasibility condition (4.72) to decrease, which makes exclusion harder. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side of invasibility condition (4.72) dominates the first fraction. In this case, increasing K_C causes the right hand side of invasibility condition (4.72) to increase, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.73) is of the form

$$f(K_C) = \frac{A}{B + CK_C}$$

where

$$A = \alpha_{RP} e_{RP} K_R$$
$$B = 1 + \frac{1}{2} e_{RP} h_{RP} K_R$$
$$C = e_{CP} h_{PC}$$

We have that $f'(K_C) < 0$. So, increasing K_C causes the first fraction on the right hand side of exclusion condition (4.73) to decrease.

The second fraction on the right hand side of exclusion condition (4.73) is of the form

$$g(K_C) = \frac{DK_C}{E + FK_C}$$

where

$$D = r_C h_{RC} \alpha_{CP} e_{CP} + \alpha_{CP} e_{CP} \alpha_{RC}$$

$$E = r_C h_{RC}$$

$$F = r_C h_{RC} e_{CP} h_{CP}$$

We have that $g'(K_C) > 0$ so increasing K_C causes the second fraction on the right hand side of exclusion condition (4.73) to increase.

So, increasing K_C causes the first fraction on the right hand side of exclusion condition (4.73) to decrease, while causing the second fraction to increase. Thus, when we add these fractions together, we get that the right hand side of exclusion condition (4.73) could be increasing or decreasing as a result of increasing K_C. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side of exclusion condition (4.73) dominates the second fraction. In this case, increasing K_C causes the right hand side of exclusion condition (4.73) to decrease, which makes exclusion easier. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side of exclusion condition (4.73) dominates the first fraction. In this case, increasing K_C causes the right hand side of exclusion condition (4.73) to increase, which makes exclusion harder. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.23. *1. We say that increasing K_R makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of K_R; i.e., if increasing K_R increases the maximum value of m_P, allowed for the predators to invade. We say that increasing K_R makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of K_R; i.e., if increasing K_R reduces the maximum value of m_P allowed for the predators to*

invade.

2. *We say that increasing K_R makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of K_R; i.e., if increasing K_R decreases the minimum value of m_P which results in the predators being excluded. We say that increasing K_R makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of K_R; i.e., if increasing K_R increases the minimum value of m_P which results in the predators being excluded.*

Theorem 4.25. *If $\frac{K_R}{2} < R^* < K_R$ then increasing K_R*

1. *makes it easier for the predator to invade if $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$.*

2. *makes it harder for the predator to invade if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$.*

3. *makes it easier for the predator to be excluded if*

   (a) *$\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) > \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$, $K_R > K_R^*$, and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$, where K_R^* is the positive solution to equation (4.74).*

   (b) *$\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) < \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$, and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$.*

4. *makes it harder for the predator to be excluded if*

   (a) *$\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) > \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$, and $0 < K_R < K_R^*$, where K_R^* is the positive solution to equation (4.74).*

   (b) *$\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) > \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$, $K_R > K_R^*$, and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$, where K_R^* is the positive solution to equation (4.74) .*

(c) $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) < \frac{1}{2}r_Ce_{RP}h_{RP}(1 +$

$e_Ch_CK_C)$, and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$.

(d) $\frac{1}{2}e_{RC}h_{RC}K_R > 1 + e_Ch_CK_C$.

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, the first fraction on the right

hand side of invasibility condition (4.68) is of the form

$$f(K_R) = \frac{AK_R + BK_R^2}{C + DK_R + EK_R^2}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}r_C(1 + e_Ch_CK_C)$$

$$B = \frac{1}{4}\alpha_{RP}e_{RP}r_Ce_{RC}h_{RC}$$

$$C = r_C(1 + e_Ch_CK_C)(1 + e_{CP}h_{PC}K_C)$$

$$D = r_C\left[e_{RP}h_{RP}(1 + e_Ch_CK_C) + \frac{1}{2}e_{RC}h_{RC}(1 + e_{CP}h_{PC}K_C)\right] + e_{CP}h_{PC}K_C\alpha_{RC}e_{RC}$$

$$E = \frac{1}{2}r_Ce_{RC}h_{RC}e_{RP}h_{RP}$$

We have that

$$f'(K_R) = \frac{(BD - AE)K_R^2 + 2BCK_R + AC}{(C + DK_R + EK_R^2)^2}.$$

We will have $f'(K_R) > 0$ if the quadratic function $q(K_R) = (BD-AE)K_R^2+2BCK_R+$

AC is positive. We will have $f'(K_R) < 0$ if $q(K_R) < 0$. The q-intercept of $q(K_R)$ is

$q = AC > 0$. The vertex of $q(K_R)$ is located at

$$K_R = -\frac{BC}{BD - AE} \begin{cases} > 0 \text{ if } BD < AE \\ \\ < 0 \text{ if } BD > AE \end{cases}.$$

If $BD > AE$ then $q(K_R)$ opens upward, the q-intercept is above the K_R-axis, and the

vertex is to the left of the q-axis. In this case, we have $f'(K_R) > 0$. But, if $BD < AE$ then $q(K_R)$ opens downward, the q-intercept is above the K_R-axis, and the vertex is to the right of the q-axis. In this case, we have $f'(K_R) > 0$ if $0 < K_R < K_R^*$ and $f'(K_R) < 0$ if $K_R > K_R^*$, where K_R^* is the positive root of $q(K_R) = 0$. Note that

$$
\begin{aligned}
BD < AE \Leftrightarrow &\frac{1}{4}\alpha_{RP}e_{RP}r_C^2 e_{RC}h_{RC}\left[e_{RP}h_{RP}(1+e_Ch_CK_C) + \frac{1}{2}e_{RC}h_{RC}(1+e_{CP}h_{PC}K_C)\right] \\
&+ \frac{1}{4}\alpha_{RP}e_{RP}r_Ce_{RC}h_{RC}e_{CP}h_{PC}K_C\alpha_{RC}e_{RC} \\
&> \frac{1}{4}r_C^2 e_{RC}h_{RC}e_{RP}h_{RP}\alpha_{RP}e_{RP}(1+e_Ch_CK_C) \\
\Leftrightarrow &\, r_C\left[e_{RP}h_{RP}(1+e_Ch_CK_C) + \frac{1}{2}e_{RC}h_{RC}(1+e_{CP}h_{PC}K_C)\right] \\
&+ e_{CP}h_{PC}K_C\alpha_{RC}e_{RC} > r_Ce_{RP}h_{RP}(1+e_Ch_CK_C) \\
\Leftrightarrow &\, \frac{1}{2}r_Ce_{RC}h_{RC}(1+e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}e_{RC} > 0
\end{aligned}
$$

and

$$
BD > AE \Leftrightarrow \frac{1}{2}r_Ce_{RC}h_{RC}(1+e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}e_{RC} < 0.
$$

So we must have $f'(K_R) > 0$. Thus, increasing K_R causes the first fraction on the right hand side of invasibility condition (4.68) to increase.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$
g(K_R) = \frac{A + BK_R}{C + DK_R + EK_R^2}
$$

where

$$A = \alpha_{CP} e_{CP} K_C r_C (1 + e_C h_C K_C)$$

$$B = \frac{1}{2} \alpha_{CP} e_{CP} K_C r_C e_{RC} h_{RC}$$

$$C = r_C (1 + e_C h_C K_C)(1 + e_{CP} h_{CP} K_C)$$

$$D = r_C \left[e_{RP} h_{RP} (1 + e_C h_C K_C) + \frac{1}{2} e_{RC} h_{RC} (1 + e_{CP} h_{CP} K_C) \right] + e_{CP} h_{CP} K_C \alpha_{RC} e_{RC}$$

$$E = \frac{1}{2} r_C e_{RC} h_{RC} e_{RP} h_{RP}$$

We have that

$$g'(K_R) = -\frac{BEK_R^2 + 2AEK_R + (DA - BC)}{(C + DK_R + EK_R^2)^2}.$$

We will have $g'(K_R) > 0$ if the quadratic function $q(K_R) = -BEK_R^2 - 2AEK_R + (BC - AD)$ is positive. We will have $g'(K_R) < 0$ if $q(K_R) < 0$. The vertex of $q(K_R)$ is located at $K_R = -\frac{A}{B} < 0$. The q-intercept of $q(K_R)$ is

$$y = BC - AD \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}.$$

If $BC < AD$ then $q(K_R)$ opens downward, the vertex is to the left of the q-axis, and the q-intercept is below the K_R-axis. In this case, we have $g'(K_R) < 0$. But if $BC > AD$ then $q(K_R)$ opens downward, the vertex is to the left of the q-axis, and the q-intercept is above the K_R-axis. In this case, we have $g'(K_R) > 0$ if $0 < K_R < K_R^*$

and $g'(K_R) < 0$ if $K_R > K_R^*$, where K_R^* is the positive root of $q(K_R) = 0$. Note that

$$BC < AD \Leftrightarrow \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C^2 e_{RC}h_{RC}(1 + e_C h_C K_C)(1 + e_{CP}h_{CP}K_C)$$

$$< \alpha_{CP}e_{CP}K_C r_C^2(1 + e_C h_C K_C)\left[h_{RP}e_{RP}(1 + e_C h_C K_C) + \frac{1}{2}e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_C)\right]$$

$$+ \alpha_{CP}e_{CP}K_C r_C e_{CP}h_{CP}K_C \alpha_{RC}e_{RC}(1 + e_C h_C K_C)$$

$$\Leftrightarrow \frac{1}{2}r_C e_{RC}h_{RC}(1 + e_C h_C K_C)(1 + e_{CP}h_{CP}K_C)$$

$$< r_C(1 + e_C h_C K_C)\left[e_{RP}h_{RP}(1 + e_C h_C K_C) + \frac{1}{2}e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_C)\right]$$

$$+ e_{CP}h_{CP}K_C \alpha_{RC}e_{RC}(1 + e_C h_C K_C)$$

$$\Leftrightarrow 0 < r_C(1 + e_C h_C K_C)^2 + e_{CP}h_{CP}K_C \alpha_{RC}e_{RC}(1 + e_C h_C K_C)$$

and

$$BC > AD \Leftrightarrow 0 > r_C(1 + e_C h_C K_C)^2 + e_{CP}h_{CP}K_C \alpha_{RC}e_{RC}(1 + e_C h_C K_C).$$

So we must have $g'(K_R) < 0$. Thus, increasing K_R causes the second fraction on the right hand side of invasibility condition (4.68) to decrease.

So, increasing K_R causes the first fraction on the right hand side of invasibility condition (4.68) to increase while causing the second fraction to decrease. When we add these fractions together, we get that the right hand side of invasibility condition (4.68) could be increasing or decreasing as a result of increasing K_R. If $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then the first fraction on the right hand side of invasibility condition (4.68) dominates the second fraction. In this case, increasing K_R causes the right hand side of invasibility condition (4.68) to increase, which makes invasion easier. But if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then the second fraction on the right hand side of invasibility condition (4.68) dominates the first fraction. In this case, increasing K_R causes the right hand side of invasibility condition (4.68) to decrease, which makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.69) is of the

form

$$f(K_R) = \frac{AK_R}{B + CK_R}$$

where

$$A = \alpha_{RP}e_{RP}$$

$$B = 1 + e_{CP}h_{PC}K_C$$

$$C = \frac{1}{2}e_{RP}h_{RP}$$

We have that $f'(K_R) > 0$, so increasing K_R causes the first fraction on the right hand side of exclusion condition (4.69) to increase.

The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$g(K_R) = \frac{A + BK_R}{C + DK_R + EK_R^2}$$

where

$$A = \alpha_{CP}e_{CP}K_C r_C (1 + e_C h_C K_C)$$

$$B = \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C e_{RC}h_{RC} + \alpha_{CP}e_{CP}K_C \alpha_{RC}e_{RC}$$

$$C = (1 + e_{CP}h_{CP}K_C)(1 + e_C h_C K_C)$$

$$D = \frac{1}{2}e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_C) + \frac{1}{2}e_{RP}h_{RP}(1 + e_C h_C K_C)$$

$$E = \frac{1}{4}e_{RP}h_{RP}e_{RC}h_{RC}$$

As in the previous case, we have that $g'(K_R) < 0$ if either $BC < AD$ or $BC > AD$ with $K_R > K_R^*$, and $g'(K_R) > 0$ if $BC > AD$ with $0 < K_R < K_R^*$, where K_R^* is the positive root of

$$-BEK_R^2 - 2AEK_R + (BC - AD) = 0. \tag{4.74}$$

Note that

$$BC < AD \Leftrightarrow \alpha_{CP}e_{CP}K_{C}e_{RC}\left(\frac{1}{2}r_{C}h_{RC} + \alpha_{RC}\right)(1 + e_{CP}h_{CP}K_{C})(1 + e_{C}h_{C}K_{C})$$

$$< \frac{1}{2}\alpha_{CP}e_{CP}K_{C}r_{C}(1 + e_{C}h_{C}K_{C})\left[e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_{C}) + e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})\right]$$

$$\Leftrightarrow e_{RC}\left(\frac{1}{2}r_{C}h_{RC} + \alpha_{RC}\right)(1 + e_{CP}h_{CP}K_{C})$$

$$< \frac{1}{2}r_{C}\left[e_{C}h_{RC}(1 + e_{CP}h_{CP}K_{C}) + e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})\right]$$

$$\Leftrightarrow \frac{1}{2}r_{C}e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_{C}) + \alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C})$$

$$< \frac{1}{2}r_{C}e_{RC}h_{RC}(1 + e_{CP}h_{CP}K_{C}) + \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$$

$$\Leftrightarrow \alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) < \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$$

and

$$BC < AD \Leftrightarrow \alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) > \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C}).$$

So, if $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) < \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C}$ with $0 < K_{R} < K_{R}^{*}$ then increasing K_{R} causes the second fraction on the right hand side of exclusion condition (4.69) to increase. But if either $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) < \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$ with $K_{R} > K_{R}^{*}$ or $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) > \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$ then increasing K_{R} causes the second fraction on the right hand side of exclusion condition (4.69) to decrease.

Therefore, if $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) > \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$ with $0 < K_{R} < K_{R}^{*}$ then increasing K_{R} causes both the first and second fractions on the right hand side of exclusion condition (4.69) to increase. So when we add these fractions together, we get that the right hand side of the exclusion condition is increasing. This makes exclusion harder. But if either $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) < \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$ or $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_{C}) < \frac{1}{2}r_{C}e_{RP}h_{RP}(1 + e_{C}h_{C}K_{C})$ with $K_{R} > K_{R}^{*}$, then increasing K_{R} causes the first fraction on the right hand side of exclusion condition (4.69) to increase, while causing the second fraction to decrease. So when we add these

fractions together, we get that the right hand side of the exclusion condition could be increasing or decreasing as a result of increasing K_R. If $\alpha_{RP}e_{RP} \gg \alpha_{CP}e_{CP}$ then the first fraction on the right hand side of exclusion condition (4.69) dominates the second fraction. In this case, increasing K_R causes the right hand side of exclusion condition (4.69) to increase. This makes invasion harder. But if $\alpha_{RP}e_{RP} \ll \alpha_{CP}e_{CP}$ then the second fraction on the right hand side of exclusion condition (4.69) dominates the first fraction. In this case, increasing K_R causes the right hand side of exclusion condition (4.69) to decrease. This makes exclusion easier.

In the case where $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$, the first fraction on the right hand side of invasibility condition (4.72) is of the form

$$f(K_R) = \frac{AK_R}{B + CK_R}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}r_C h_{RC}$$
$$B = r_C h_{RC}(1 + e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}$$
$$C = r_C h_{RC}e_{RP}h_{RP}$$

We have that $f'(K_R) > 0$, so increasing K_R causes first fraction on the right hand side of invasibility condition (4.72) to increase.

The second fraction on the right hand side of invasibility condition (4.72) is of the form

$$g(K_R) = \frac{D}{E + FK_R}$$

where

$$D = \alpha_{CP} e_{CP} K_C r_C h_{RC}$$

$$E = r_C(1 + e_{CP} h_{CP} K_C) + e_{CP} h_{CP} K_C \alpha_{RC}$$

$$F = r_C h_{RC} e_{RP} h_{RP}$$

We have that $g'(K_R) < 0$, so increasing K_R causes the second fraction on the right hand side of invasibility condition (4.72) to decrease.

So, increasing K_R causes the first fraction on the right hand side of invasibility condition (4.72) to increase, while causing the second fraction to decrease. So when we add these fractions together, we get that the right hand side of invasibility condition (4.72) could be increasing or decreasing as a result of increasing K_R. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side of invasibility condition (4.72) dominates the second fraction. In this case, increasing K_R causes the right hand side of invasibility condition (4.72) to increase, which makes invasion easier. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side of invasibility condition (4.72) dominates the first fraction. In this case, increasing K_R causes the right hand side of invasibility condition (4.72) to decrease. This makes invasion harder.

The second fraction on the right hand side of exclusion condition (4.73) is independent of K_R. The first fraction on the right hand side of exclusion condition (4.73) is of the form

$$f(K_R) = \frac{AK_R}{B + CK_R}$$

where

$$A = \alpha_{RP} e_{RP}$$

$$B = 1 + e_{CP} h_{PC} K_C$$

$$C = \frac{1}{2} e_{PR} h_{RP}$$

We have that $f'(K_R) > 0$ so increasing K_R causes the right hand side of exclusion condition (4.73) to increase, which makes exclusion harder. □

Before stating the following theorem, we introduce some terminology.

Definition 4.24.   *1. We say that increasing α_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of α_{RC}; i.e., if increasing α_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing α_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of α_{RC}; i.e., if increasing α_{RC} reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing α_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of α_{RC}; i.e., if increasing α_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing α_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of α_{RC}; i.e., if increasing α_{RC} increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.26. *If $\frac{K_R}{2} < R^* < K_R$ then increasing α_{RC}*

1. *makes it harder for the predator to invade.*

2. *makes it harder for the predator to be excluded.*

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(\alpha_{RC}) = \frac{A}{B + \alpha_{RC}}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_Rr_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_Ch_CK_C\right)$$

$$B = r_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_Ch_CK_C\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$C = e_{CP}h_{PC}K_Ce_{RC}K_R$$

We have that $f'(\alpha_{RC}) < 0$, so increasing α_{RC} causes the first fraction on the right hand side of invasibility condition (4.68) to decrease.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$g(\alpha_{RC}) = \frac{D}{E + F\alpha_{RC}}$$

where

$$D = \alpha_{CP}e_{CP}K_Cr_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_Ch_CK_C\right)$$

$$E = r_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_Ch_CK_C\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

$$F = e_{CP}h_{CP}K_Ce_{RC}K_R$$

We have that $g'(\alpha_{RC}) < 0$, so increasing α_{RC} causes the second fraction on the right hand side of invasibility condition (4.68) to decrease.

So, increasing α_{RC} causes both the first and second fractions on the right hand side of invasibility condition (4.68) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.69) is independent of α_{RC}. The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$f(\alpha_{RC}) = A + B\alpha_{RC}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}{\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C e_{RC}K_R}{\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}$$

We have that $f'(\alpha_{RC}) > 0$, so increasing α_{RC} causes the right hand side of exclusion condition (4.69) to increase. This makes exclusion harder.

In the case where $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$, the first fraction on the right hand side of invasibility condition (4.72) is of the form

$$f(\alpha_{RC}) = \frac{A}{B + C\alpha_{RC}}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C h_{RC}$$

$$B = r_C h_{RC}(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$C = e_{CP}h_{PC}K_C$$

We have that $f'(\alpha_{RC}) < 0$, so increasing α_{RC} causes the first fraction on the right hand side of invasibility condition (4.72) to decrease.

The second fraction on the right hand side of invasibility condition (4.72) is of the

form

$$g(\alpha_{RC}) = \frac{D}{E + F\alpha_{RC}}$$

where

$$D = \alpha_{CP}e_{CP}K_C r_C h_{RC}$$

$$E = r_C h_{RC}(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

$$F = e_{CP}h_{CP}K_C$$

We have that $g'(\alpha_{RC}) < 0$, so increasing α_{RC} causes the second fraction on the right hand side of invasibility condition (4.72) to decrease.

So, increasing α_{RC} causes both the first and second fractions on the right hand side of invasibility condition (4.72) to decrease. So when we add these fractions together, we get that the right hand side of invasibility condition (4.72) is decreasing as a result of increasing α_{RC}. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.73) is independent of α_{RC}. The second fraction on the right hand side of exclusion condition (4.73) is of the form

$$f(\alpha_{RC}) = A + B\alpha_{RC}$$

where

$$A = \frac{r_C h_{RC}\alpha_{CP}e_{CP}K_C}{r_C h_{RC}(1 + e_{CP}h_{CP}K_C)}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C}{r_C h_{RC}(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(\alpha_{RC}) > 0$ so increasing α_{RC} causes the right hand side of exclusion condition (4.73) to increase, which makes exclusion harder. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.25. *1. We say that increasing ea_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of e_{RC}; i.e., if increasing e_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing e_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of e_{RC}; i.e., if increasing e_{RC} reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing e_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of e_{RC}; i.e., if increasing e_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing e_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of e_{RC}; i.e., if increasing e_{RC} increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.27. *If $\frac{K_R}{2} < R^{*} < K_R$ then increasing e_{RC}*

1. makes it harder for the predator to invade if $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$.

2. makes it harder for the predator to be excluded if $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$.

3. has no effect on whether the predator can invade or is excluded from the system if $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$.

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(e_{RC}) = \frac{A + Be_{RC}}{C + De_{RC}}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C(1 + e_C h_C K_C)$$

$$B = \frac{1}{4}\alpha_{RP}e_{RP}K_R^2 r_C h_{RC}$$

$$C = r_C(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$D = \frac{1}{2}r_C h_{RC}K_R(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}K_R$$

We have that

$$f'(e_{RC}) = \frac{BC - AD}{(C + De_{RC})^2} \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}$$

Note that

$$BC > AD \Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C^2 h_{RC}(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$> \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C^2 h_{RC}(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)(1 + e_C h_C K_C)$$

$$+ \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C e_{CP}h_{PC}K_C\alpha_{RC}(1 + e_C h_C K_C)$$

$$\Leftrightarrow 0 > \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C e_{CP}h_{PC}K_C\alpha_{RC}(1 + e_C h_C K_C)$$

and

$$BC < AD \Leftrightarrow 0 < \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C e_{CP}h_{PC}K_C\alpha_{RC}(1 + e_C h_C K_C).$$

So, $f'(e_{RC}) < 0$ for all biologically relevant values of the parameters. Thus, increasing e_{RC} causes the first fraction on the right hand side of invasibility condition (4.68) to decrease.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$g(e_{RC}) = \frac{E + Fe_{RC}}{G + He_{RC}}$$

where

$$E = \alpha_{CP} e_{CP} K_C r_C (1 + e_C h_C K_C)$$

$$F = \frac{1}{2} \alpha_{CP} e_{CP} K_C r_C h_{RC} K_R$$

$$G = r_C (1 + e_C h_C K_C)(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

$$H = \frac{1}{2} r_C h_{RC} K_R (1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C) + e_{CP} h_{CP} K_C \alpha_{RC} K_R$$

We have that $g'(e_{RC}) > 0$ if $FG > EH$ and $g'(e_{RC}) < 0$ if $FG < EH$. Note that

$$
\begin{aligned}
FG > EH \Leftrightarrow{} & \frac{1}{2} \alpha_{CP} e_{CP} K_C r_C^2 h_{RC} K_R (1 + e_C h_C K_C)(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C) \\
> {}& \frac{1}{2} \alpha_{CP} e_{CP} K_C r_C^2 h_{RC} K_R (1 + e_C h_C K_C)(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C) \\
& + \alpha_{CP} e_{CP}^2 K_C^2 r_C h_{CP} \alpha_{RC} K_R (1 + e_C h_C K_C) \\
\Leftrightarrow{} & 0 > \alpha_{CP} e_{CP}^2 K_C^2 r_C h_{CP} \alpha_{RC} K_R (1 + e_C h_C K_C)
\end{aligned}
$$

and

$$FG < EH \Leftrightarrow 0 < \alpha_{CP} e_{CP}^2 K_C^2 r_C h_{CP} \alpha_{RC} K_R (1 + e_C h_C K_C).$$

So we must have $g'(e_{RC}) < 0$ for all biologically relevant values of the parameter. Thus, increasing e_{RC} causes the second fraction on the right hand side of invasibility condition (4.68) to decrease.

Thus, increasing e_{RC} causes both the first and second fractions on the right hand side of invasibility condition (4.68) to decrease. So when we add these fractions together, we get that increasing e_{RC} causes the right hand side of invasibility condition (4.68) to decrease. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (4.69) is independent of e_{RC}. The second fraction on the right hand side of exclusion condition (4.69)

is of the form

$$f(e_{RC}) = \frac{A + Be_{RC}}{C + De_{RC}}$$

where

$$A = \alpha_{CP}e_{CP}K_C r_C (1 + e_C h_C K_C)$$

$$B = \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C h_{RC}K_R + \alpha_{CP}e_{CP}K_C \alpha_{RC}K_R$$

$$C = \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$D = \frac{1}{2}h_{RC}K_R \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)$$

We have that $f'(e_{RC}) > 0$ if $BC > AD$ and $f'(e_{RC}) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \alpha_{CP}e_{CP}K_C K_R \left(\frac{1}{2}r_C h_{RC} + \alpha_{RC}\right)\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$> \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C h_{RC}K_R \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$\Leftrightarrow \frac{1}{2}r_C h_{RC} + \alpha_{RC} > \frac{1}{2}r_C h_{RC}$$

$$\Leftrightarrow \alpha_{RC} > 0$$

and

$$BC < AD \Leftrightarrow \alpha_{RC} < 0.$$

So, we have that $f'(e_{RC}) > 0$ so increasing e_{RC} causes the right hand side of exclusion condition (4.69) to increase, which makes exclusion harder.

In the case where $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_C$, none of the fractions on the right hand side of either invasibility condition (4.72) or exclusion condition (4.73) depends on e_{RC}. □

Before stating the following theorem, we introduce some terminology.

Definition 4.26.   *1. We say that increasing h_{RC} makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56)*

is an increasing function of h_{RC}; i.e., if increasing h_{RC} increases the maximum value of m_P, allowed for the predators to invade. We say that increasing h_{RC} makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of h_{RC}; i.e., if increasing h_{RC} reduces the maximum value of m_P allowed for the predators to invade.

2. *We say that increasing h_{RC} makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of h_{RC}; i.e., if increasing h_{RC} decreases the minimum value of m_P which results in the predators being excluded. We say that increasing h_{RC} makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of h_{RC}; i.e., if increasing h_{RC} increases the minimum value of m_P which results in the predators being excluded.*

Theorem 4.28. *If $\frac{K_R}{2} < R^* < K_R$ then increasing h_{RC}*

1. *makes it easier for the predator to invade.*

2. *makes it easier for the predator to be excluded.*

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(h_{RC}) = \frac{A + Bh_{RC}}{C + Dh_{RC}}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C(1 + e_C h_C K_C)$$

$$B = \frac{1}{4}\alpha_{RP}e_{RP}K_R^2 r_C e_{RC}$$

$$C = r_C(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C\alpha_{RC}e_{RC}K_R$$

$$D = \frac{1}{2}r_C e_{RC}K_R(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

We have that

$$f'(h_{RC}) \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}.$$

Note that

$$
\begin{aligned}
BC > AD \Leftrightarrow & \frac{1}{4}\alpha_{RP}e_{RP}K_R^2 r_C^2 e_{RC}(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) \\
& + \frac{1}{4}\alpha_{RP}e_{RP}K_R^3 r_C e_{RC}^2 e_{CP}h_{PC}K_C\alpha_{RC} \\
& > \frac{1}{4}\alpha_{RP}e_{RP}K_R^2 r_C^2 e_{RC}(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) \\
\Leftrightarrow & \frac{1}{4}\alpha_{RP}e_{RP}K_R^3 r_C e_{RC}^2 e_{CP}h_{PC}K_C\alpha_{RC} > 0
\end{aligned}
$$

and

$$BC < AD \Leftrightarrow \frac{1}{4}\alpha_{RP}e_{RP}K_R^3 r_C e_{RC}^2 e_{CP}h_{PC}K_C\alpha_{RC}.$$

So we have $f'(h_{RC}) > 0$. Therefore, increasing h_{RC} causes the first fraction on the right hand side of invasibility condition (4.68) to increase.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$g(h_{RC}) = \frac{E + Fh_{RC}}{G + Hh_{RC}}$$

where

$$E = \alpha_{CP}e_{CP}K_C r_C(1 + e_C h_C K_C)$$

$$F = \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C e_{RC}K_R$$

$$G = r_C(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R$$

$$H = \frac{1}{2}r_C e_{RC}K_R(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

We have that

$$g'(h_{RC}) \begin{cases} > 0 \text{ if } FG > EH \\ \\ < 0 \text{ if } FG < EH \end{cases}.$$

Note that

$$\begin{aligned}
FG > EH \Leftrightarrow \; &\frac{1}{2}\alpha_{CP}e_{CP}K_C r_C^2 e_{RC}K_R(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) \\
&+ \frac{1}{2}\alpha_{CP}e_{CP}^2 K_C^2 r_C e_{RC}^2 K_R^2 h_{CP}\alpha_{RC} \\
&> \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C^2 e_{RC}K_R(1 + e_C h_C K_C)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) \\
\Leftrightarrow \; &\frac{1}{2}\alpha_{CP}e_{CP}^2 K_C^2 r_C e_{RC}^2 K_R^2 h_{CP}\alpha_{RC} > 0
\end{aligned}$$

and

$$FG < EH \Leftrightarrow \frac{1}{2}\alpha_{CP}e_{CP}^2 K_C^2 r_C e_{RC}^2 K_R^2 h_{CP}\alpha_{RC} < 0.$$

So we have that $g'(h_{RC}) > 0$. Therefore, increasing h_{RC} causes the second fraction on the right hand side of invasibility condition (4.68) to increase.

Thus, increasing h_{RC} causes both the first and second fractions on the right hand side of invasibility condition (4.68) to increase. So when we add these fractions together, we get that the right hand side of the invasibility condition is increasing as a result of increasing h_{RC}. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.69) is indepen-

dent of h_{RC}. The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$f(h_{RC}) = \frac{A + Bh_{RC}}{C + Dh_{RC}}$$

where

$$A = \alpha_{CP}e_{CP}K_C r_C(1 + e_C h_C K_C) + \alpha_{CP}e_{CP}K_C \alpha_{RC}e_{RC}K_R$$

$$B = \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C e_{RC}K_R$$

$$C = \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$D = \frac{1}{2}e_{RC}K_R\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)$$

We have that

$$f'(h_{RC}) \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}.$$

Note that

$$BC > AD \Leftrightarrow \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C e_{RC}K_R\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$> \frac{1}{2}\alpha_{CP}e_{CP}K_C r_C e_{RC}K_R\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)(1 + e_C h_C K_C)$$

$$+ \frac{1}{2}\alpha_{CP}e_{CP}K_C \alpha_{RC}e_{RC}^2 K_R^2\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)$$

$$\Leftrightarrow 0 > \frac{1}{2}\alpha_{CP}e_{CP}K_C \alpha_{RC}e_{RC}^2 K_R^2\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)$$

and

$$BC < AD \Leftrightarrow 0 < \frac{1}{2}\alpha_{CP}e_{CP}K_C \alpha_{RC}e_{RC}^2 K_R^2\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right).$$

So we have that $f'(h_{RC}) < 0$. Thus, increasing h_{RC} causes the right hand side of exclusion condition (4.69) to decrease, which makes exclusion easier.

In the case where $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$, the first fraction on the right hand side of invasibility condition (4.72) is of the form

$$f(h_{RC}) = \frac{A h_{RC}}{B + C h_{RC}}$$

where

$$A = \frac{1}{2} \alpha_{RP} e_{RP} K_R r_C$$

$$B = r_C(1 + e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C)$$

$$C = e_{CP} h_{PC} K_C \alpha_{RC}$$

We have that $f'(h_{RC}) > 0$, so increasing h_{RC} causes the first fraction on the right hand side of invasibility condition (4.72) to increase.

The second fraction on the right hand side of invasibility condition (4.72) is of the form

$$g(h_{RC}) = \frac{D h_{RC}}{E + F h_{RC}}$$

where

$$D = \frac{1}{2} \alpha_{RP} e_{RP} K_R r_C$$

$$E = r_C(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

$$F = e_{CP} h_{CP} K_C \alpha_{RC}$$

We have that $g'(h_{RC}) > 0$, so increasing h_{RC} causes the second fraction on the right hand side of invasibility condition (4.72) to increase.

Thus, increasing h_{RC} causes both the first and second fractions on the right hand side of invasibility condition (4.72) to increase. When we add these fractions together, we get that the right hand side is increasing. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.73) is independent of h_{RC}. The second fraction on the right hand side of exclusion condition (4.72) is of the form

$$f(h_{RC}) = A + \frac{B}{h_{RC}}$$

where

$$A = \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$$
$$B = \frac{\alpha_{CP} e_{CP} K_C \alpha_{RC}}{r_C(1 + e_{CP} h_{CP} K_C)}$$

We have that $f'(h_{RC}) < 0$. So, increasing h_{RC} causes the right hand side of exclusion condition (4.73) to decrease, which makes exclusion easier. □

Before stating the following theorem, we introduce some terminology.

Definition 4.27. *1. We say that increasing $e_C h_C$ makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ increases the maximum value of m_P, allowed for the predators to invade. We say that increasing $e_C h_C$ makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing $e_C h_C$ makes it easier for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of $e_C h_C$; i.e., if increasing $e_C h_C$ decreases the minimum value of m_P which results in the predators being excluded. We say that increasing $e_C h_C$ makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of $e_C h_C$; i.e.,

if increasing $e_C h_C$ increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.29. *If $\frac{K_R}{2} < R^* < K_R$ then increasing $e_C h_C$*

1. *makes it easier for the predators to invade if $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$.*

2. *makes it easier for the predators to be excluded if $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$.*

3. *has no effect on whether the predators can invade or are excluded, if $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$.*

Proof. In the case where $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(e_C h_C) = \frac{A + B e_C h_C}{C + D e_C H_C}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$B = \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C K_C$$

$$C = r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C) + e_{CP}h_{PC}K_C \alpha_{RC}e_{RC}K_R$$

$$D = r_C K_C (1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

We have that

$$f'(e_C h_C) \begin{cases} > 0 \text{ if } BC > AD \\ \\ < 0 \text{ if } BC < AD \end{cases}.$$

Note that

$$BC > AD \Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C^2 K_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$+ \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C K_C^2 e_{CP}h_{PC}\alpha_{RC}e_{RC}$$

$$> \frac{1}{2}\alpha_{RP}e_{RP}K_R r_C^2 K_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C)$$

$$\Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C K_C^2 e_{CP}h_{PC}\alpha_{RC}e_{RC} > 0$$

and

$$BC < AD \Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R^2 r_C K_C^2 e_{CP}h_{PC}\alpha_{RC}e_{RC} < 0.$$

So we have that $f'(e_C h_C) > 0$. So, increasing $e_C h_C$ causes the first fraction on the right hand side of invasibility condition (4.68) to increase.

The second fraction on the right hand side of invasibility condition (4.68) is of the form

$$g(e_C h_C) = \frac{E + F e_C h_C}{G + H e_C h_C}$$

where

$$E = \alpha_{CP}e_{CP}K_C r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$

$$F = \alpha_{CP}e_{CP}K_C^2 r_C$$

$$G = r_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C) + e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R$$

$$H = r_C K_C(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

We have that

$$g'(e_C h_C) \begin{cases} > 0 \text{ if } FG > EH \\ \\ < 0 \text{ if } FG < EH \end{cases}.$$

Note that

$$FG > EH \Leftrightarrow \alpha_{CP} e_{CP} K_C^2 r_C^2 \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) (1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

$$+ \alpha_{CP} e_{CP}^2 K_C^3 r_C h_{CP} \alpha_{RC} e_{RC} K_R$$

$$> \alpha_{CP} e_{CP} K_C^2 r_C^2 \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) (1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

$$\Leftrightarrow \alpha_{CP} e_{CP}^2 K_C^3 r_C h_{CP} \alpha_{RC} e_{RC} K_R > 0$$

and

$$FG < EH \Leftrightarrow \alpha_{CP} e_{CP}^2 K_C^3 r_C h_{CP} \alpha_{RC} e_{RC} K_R < 0.$$

So we have that $g'(e_C h_C) > 0$. So, increasing $e_C h_C$ causes the second fraction on the right hand side of invasibility condition (4.68) to increase.

Thus, increasing $e_C h_C$ causes both the first and second fractions on the right hand side of invasibility condition (4.68) to increase. So when we add these fractions together, the right hand side of invasibility condition (4.68) is increasing as a result of increasing $e_C h_C$. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.69) is independent of $e_C h_C$. The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$f(e_C h_C) = \frac{A + B e_C h_C}{C + D e_C H_C}$$

where

$$A = \alpha_{CP} e_{CP} K_C r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) + \alpha_{CP} e_{CP} K_C \alpha_{RC} e_{RC} K_R$$

$$B = \alpha_{CP} e_{CP} K_C^2 r_C$$

$$C = \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right) \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)$$

$$D = K_C \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right)$$

We have that $f'(e_C h_C) > 0$ if $BC > AD$ and $f'(e_C h_C) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \alpha_{CP} e_{CP} K_C^2 r_C \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right) \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)$$
$$> \alpha_{CP} e_{CP} K_C^2 r_C \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right)$$
$$+ \alpha_{CP} e_{CP} K_C^2 \alpha_{RC} e_{RC} K_R \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right)$$
$$\Leftrightarrow 0 > \alpha_{CP} e_{CP} K_C^2 \alpha_{RC} e_{RC} K_R \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right)$$

and

$$BC < AD \Leftrightarrow 0 < \alpha_{CP} e_{CP} K_C^2 \alpha_{RC} e_{RC} K_R \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C\right).$$

So we have that $f'(e_C h_C) < 0$. So, increasing $e_C h_C$ causes the right hand side of exclusion condition (4.69) to decrease, which makes exclusion easier.

In the case where $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$, none of the fractions on the right hand side of either invasibility condition (4.72) or exclusion condition (4.73) depends on $e_C h_C$. So, increasing $e_C h_C$ has no effect on whether the predators are able to invade or are excluded from the system. $\square$

Before stating the following theorem, we introduce some terminology.

Definition 4.28. *1. We say that increasing r_C makes it easier for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is an increasing function of r_C; i.e., if increasing r_C increases the maximum value of m_P, allowed for the predators to invade. We say that increasing r_C makes it harder for the predators to invade if the right hand side of either invasibility condition (4.54) or (4.56) is a decreasing function of r_C; i.e., if increasing r_C reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing r_C makes it easier for the predators to be excluded if

the right hand side of either exclusion condition (4.55) or (4.57) is a decreasing function of r_C; i.e., if increasing r_C decreases the minimum value of m_P which results in the predators being excluded. We say that increasing r_C makes it harder for the predators to be excluded if the right hand side of either exclusion condition (4.55) or (4.57) is an increasing function of r_C; i.e., if increasing r_C increases the minimum value of m_P which results in the predators being excluded.

Theorem 4.30. *If $\frac{K_R}{2} < R^* < K_R$ then increasing r_C*

1. *makes it easier for the predators to invade.*

2. *makes it easier for the predators to be excluded if $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$.*

3. *makes it harder for the predators to be excluded if $\frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$.*

Proof. In the case where $\frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$, the first fraction on the right hand side of invasibility condition (4.68) is of the form

$$f(r_C) = \frac{A r_C}{B + C r_C}$$

where

$$A = \frac{1}{2} \alpha_{RP} e_{RP} K_R \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C \right)$$

$$B = e_{CP} h_{PC} K_C \alpha_{RC} e_{RC} K_R$$

$$C = \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_C h_C K_C \right) \left(1 + e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C \right)$$

We have that $f'(r_C) > 0$, so increasing r_C causes the first fraction on the right hand side of invasibility condition (4.68) to increase.

The second fraction on the right hand side of invasibility condition (4.68) is of the

form

$$g(r_C) = \frac{Dr_C}{E + Fr_C}$$

where

$$D = \alpha_{CP}e_{CP}K_C \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)$$

$$E = e_{CP}h_{CP}K_C\alpha_{RC}e_{RC}K_R$$

$$F = \left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C)$$

We have that $g'(r_C) > 0$, so increasing r_C causes the second fraction on the right hand side of invasibility condition (4.68) to increase.

Thus, increasing r_C causes both the first and second fractions on the right hand side of invasibility condition (4.68) to increase. So, when we add these fractions together, we get that the right hand side of invasibility condition (4.68) is increasing, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.69) is independent of r_C. The second fraction on the right hand side of exclusion condition (4.69) is of the form

$$f(r_C) = A + Br_C$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}e_{RC}K_R}{\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\right)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C K_C\right)}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C}$$

We have that $f'(r_C) > 0$, so increasing r_C causes the right hand side of exclusion condition (4.69) to increase. This makes invasion harder.

In the case where $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$, the first fraction on the right hand

side of invasibility condition (4.72) is of the form

$$f(r_C) = \frac{A r_C}{B + C r_C}$$

where

$$A = \frac{1}{2} \alpha_{RP} e_{RP} K_R h_{RC}$$

$$B = e_{CP} h_{PC} K_C \alpha_{RC}$$

$$C = h_{RC}(1 + e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C)$$

We have that $f'(r_C) > 0$, so increasing r_C causes the first fraction on the right hand side of invasibility condition (4.72) to increase.

The second fraction on the right hand side of invasibility condition (4.72) is of the form

$$f(r_C) = \frac{D r_C}{E + F r_C}$$

where

$$D = \alpha_{CP} e_{CP} K_C h_{RC}$$

$$E = e_{CP} h_{CP} K_C \alpha_{RC}$$

$$F = h_{RC}(1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C)$$

We have that $g'(r_C) > 0$, so increasing r_C causes the second fraction on the right hand side of invasibility condition (4.72) to increase.

Thus, increasing r_C causes both the first and second fractions on the right hand side of invasibility condition (4.72) to increase. When we add these fractions together, we get that the right hand side of invasibility condition (4.72) is increasing, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (4.73) is independent of r_C. The second fraction on the right hand side of exclusion condition (4.73) is of the form

$$f(r_C) = A + \frac{B}{r_C}$$

where

$$A = \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

$$B = \frac{\alpha_{CP}e_{CP}K_C\alpha_{RC}}{h_{RC}(1 + e_{CP}h_{CP}K_C)}$$

We have that $f'(r_C) < 0$, so increasing r_C causes the right hand side of exclusion condition (4.73) to decrease. This makes exclusion easier. $\square$

4.8.3 $\quad K_R \left(1 - \frac{e_{RC}}{r_C e_C h_C}\right) < R^* < K_R$

If $K_R \left(1 - \frac{e_{RC}}{r_C e_C h_C}\right) < R^* < K_R$ and $e_{RC}^2 h_{RC} K_R < r_R e_C h_C (1 + e_C h_C K_C)$ then we use the bounds on C^* imposed by the supersolution to the consumer equation, given by inequalities (4.29). In this case, invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{RP}e_{RP}K_R \left(1 - \frac{e_{RC}}{r_R e_C h_C}\right)}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C \left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C \left[1 + e_{RC}h_{RC}K_R\left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C\right]}\right)}$$

$$+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C \left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C \left[1 + e_{RC}h_{RC}K_R\left(1 - \frac{e_{RC}}{r_R e_C h_C}\right) + e_C h_C K_C\right]}\right)}$$

$$(4.75)$$

and exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right) + e_{CP}h_{PC}K_C}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C\left[1 + e_{RC}h_{RC}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right) + e_Ch_CK_C\right]}\right)}{1 + e_{RP}h_{RP}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right) + e_{CP}h_{CP}K_C} \quad (4.76)$$

If $K_R\left(1 - \frac{e_{RC}}{r_Ce_Ch_C}\right) < R^* < K_R$ and $r_Re_Ch_C(1 + e_Ch_CK_C) < e_{RC}^2h_{RC}K_R$ (which implies that $r_Re_Ch_C(1 + e_Ch_CK_C) < e_{RC}h_{RC}K_Rr_Re_Ch_C$, which is equivalent to $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$) then we use the bounds on C^* imposed by the consumer isocline's horizontal asymptote, given by inequalities (4.30). In this case, invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{RP}e_{RP}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right)}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_Ch_{RC}}\right)}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_Ch_{RC}}\right)} \quad (4.77)$$

and exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right) + e_{CP}h_{PC}K_C}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_Ch_{RC}}\right)}{1 + e_{RP}h_{RP}K_R\left(1 - \frac{e_{RC}}{r_Re_Ch_C}\right) + e_{CP}h_{CP}K_C}. \quad (4.78)$$

Note that whether the predator is able to invade or is excluded from the system depends in part on parameters which are independent of the predator itself. If changing these parameters causes the right hand side of the invasion condition to increase, then invasion becomes easier, which decreasing the right hand side makes invasion harder. On the other hand, if changes to these parameters cause the right hand side

of the exclusion condition to increase, then that means it will be harder to exclude the predator, while a decrease would mean that exclusion is easier.

While the dependence of the invasibility and exclusion conditions on the parameters in this case could prove interesting, the calculations and expressions become prohibitively long and complicated, and drawing useful conclusions becomes difficult. It would, however, be worth exploring further in the future.

Boundary Limit Cycle

Now suppose we have the ω-periodic solution $(\Gamma_R, \Gamma_C, 0)$, which is unstable in the (R, C)-plane. The Floquet multiplier in the P direction is given by

$$\exp\left[\frac{1}{\omega}\int_0^\omega \left(\frac{\alpha_{RP}\Gamma_R(t)}{1 + h_{RP}\Gamma_R(t) + h_{PC}\Gamma_C(t)} + \frac{\alpha_{CP}\Gamma_C(t)}{1 + h_{RP}\Gamma_R(t) + h_{CP}\Gamma_C(t)} - m_P\right) dt\right].$$

Thus, if (in dimensionalized terms)

$$m_P < \int_0^\omega \left(\frac{\alpha_{RP}e_{RP}\Gamma_R(t)}{1 + e_{RP}h_{RP}\Gamma_R(t) + e_{CP}h_{PC}\Gamma_C(t)} + \frac{\alpha_{CP}e_{CP}\Gamma_C(t)}{1 + e_{RP}h_{RP}\Gamma_R(t) + e_{CP}h_{CP}\Gamma_C(t)}\right) dt \tag{4.79}$$

then $(\Gamma_R, \Gamma_C, 0)$ is unstable in the P direction.

4.9 Permanence

For permanence, the only thing that remains to show is acyclicity. We will now take $Y_0 = \mathbb{R}^3_+$ so that (now using dimensionzalied parameters) $\partial Y_0 = \Big\{(R, C, 0) : R \geq 0, C \geq 0\Big\} \cup \{(R, 0, P) : R \geq 0, P \geq 0\} \cup \{(0, C, P) : C \geq 0, P \geq 0\}$. Then $\omega(\partial Y_0)$ always includes the equilibria $(0, 0, 0), (K_R, 0, 0)$, and $(0, K_C, 0)$. Additionally, when they exist, $\omega(\partial Y_0)$ includes the equilibria of the form $(R^*, C^*, 0)$, of which there can be one, two, or three, $(R^*, 0, P^*)$, and $(0, C^*, P^*)$, or the periodic boundary solution $(\gamma_R, \gamma_C, 0), (\phi_R, 0, \phi_P)$, and $(0, \psi_C, \psi_P)$.

We know from section 4.3 that $(0,0,0)$ is a saddle, where the (R,C)-plane is the unstable subspace and the P-axis is the stable subspace.

If (3.7) holds, then $(K_R,0,0)$, restricted to the (R,P)-plane, is a saddle with the R-axis being the stable subspace and the P-axis being the unstable subspace. In this case, the equilibrium $\left(R^*,0,P^*\right)$ exists and the system is permanent in the (R,P)-plane. Thus, there will be no heteroclinic orbit starting at $\left(R^*,0,P^*\right)$ and connecting to another equilibrium. So if there is a heteroclinic orbit in the (R,P)-plane from $(K_R,0,0)$ to $\left(R^*,0,P^*\right)$ then it will not be able to connect to any other heteroclinic orbit in ∂Y_0. If (3.7) does not hold, then $(K_R,0,0)$, when restricted to the (R,P)-plane, is a stable node so the equilibrium $\left(R^*,0,P^*\right)$ does not exist. In this case, there could be a heteroclinic orbit starting at $(0,0,0)$ and ending at $(K_R,0,0)$.

If (3.3) holds, then $(0,K_C,0)$, restricted to the (C,P)-plane, is a saddle with the C-axis being the stable subspace and the P-axis being the unstable subspace. In this case, the equilibrium $\left(0,C^*,P^*\right)$ exists and the system is permanent in the (C,P)-plane. Thus, there will be no heteroclinic orbit starting at $\left(0,C^*,P^*\right)$ and connecting to another equilibrium. So if there is a heteroclinic orbit in the (C,P)-plane from $(0,K_C,0)$ to $\left(0,C^*,P^*\right)$ then it will not be able to connect to any other heteroclinic orbit in ∂Y_0. If (3.3) does not hold, then $(0,K_C,0)$ is a stable node in the (C,P)-plane and the equilibrium $\left(0,C^*,P^*\right)$ does not exist. In this case, there could be a heteroclinic orbit starting at $(0,0,0)$ and ending at $(0,K_C,0)$.

Since the possible heteroclinic orbit in the (R,P)-plane and the possible heteroclinic orbit in the (C,P)-plane both need to start at $(0,0,0)$, they cannot be both be part of a heteroclinic orbit which forms a heteroclinic cycle in ∂Y_0. In fact, the only possible heteroclinic cycle either could be part of would be one that has part of its trajectory in the (R,C)-plane and ends at $(0,0,0)$. But since the (R,C)-plane is the unstable subspace of $(0,0,0)$, no heteroclinic orbit in the (R,C)-plane can end at $(0,0,0)$. Thus, no heteroclinic cycles are possible in ∂Y_0 so the system is acyclic.

Thus, we have proved the following result.

Theorem 4.31. *If the boundary equilibria exist, the system (4.1) is permanent provided that (4.35), (4.43), (4.52), and at least one of (4.32) or (4.33) holds.*

Remarks:

1. The consumers can always invade the system at $(K_R, 0, 0)$. So inequality (4.31) does not affect the permanence of the system.

2. If both (4.32) and (4.33) hold, in addition to the other conditions, then the system is permanent. But if only (4.32) holds then the predator still has the opportunity to invade the $R - C$ subsystem if (4.52) holds. So the system can still be permanent even if (4.33) does not hold. If only (4.33) holds then the resource still has the opportunity to invade the $C - P$ subsystem when (4.35) holds. So the system can still be permanent even when (4.32) does not hold.

Chapter 5

Analysis of the Full Model with Harvesting

We now consider the cases where we have harvesting in the system. Note that we can rewrite the system as

$$
\frac{dR}{dt} = (r_R - H_R)R\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C + e_{CP}h_{PC}P}
$$
$$
- \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P}
$$
$$
\frac{dC}{dt} = (r_C - H_C)C\left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right)K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C + e_{CP}h_{PC}P}
$$

$$(5.1)$$

$$
- \frac{e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P}
$$
$$
\frac{dP}{dt} = \frac{\alpha_{RP}e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} + \frac{\alpha_{CP}e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P}
$$
$$
- (m_P + H_P)P
$$

5.1 Harvesting the $C - P$ Subsystem

5.1.1 Harvesting only the Consumers

In this case, the form of the subsystem is

$$\frac{dC}{dt} = (r_C - H_C)C \left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C} \right) K_C} \right) - \frac{e_{CP}CP}{1 + e_{CP}h_{CP}C + e_Ph_PP} \tag{5.2}$$

$$\frac{dP}{dt} = \frac{\alpha_{CP}e_{CP}CP}{1 + e_{CP}h_{CP}C + e_Ph_PP} - m_PP$$

There are three possibly biologically relevant equilibria for this subsystem: $(0,0)$, $\left(\left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$, and (C^*, P^*), where

$$C^* = \frac{\beta + \sqrt{\beta^2 + 4\alpha_{CP}e_Ph_Pm_P \left(\frac{(r_C - H_C)^2}{r_C} \right) K_C}}{2(r_C - H_C)\alpha_{CP}e_Ph_P}$$

for

$$\beta = \frac{(r_C - H_C)^2}{r_C}K_C\alpha_{CP}e_Ph_P + e_{CP}h_{CP}m_P \left(\frac{r_C - H_C}{r_C} \right) K_C - \alpha_{CP}e_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C$$

and

$$P^* = \frac{\alpha_{CP}e_{CP}C^* - m_P \left(1 + e_{CP}h_{CP}C^* \right)}{e_Ph_Pm_P}$$

Note that in order for $\left(\left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$ to be biologically relevant, we must have $H_C < r_C$ and in order for (C^*, P^*) to be biologically relevant, we must have

$$P^* > 0 \Leftrightarrow \alpha_{CP}e_{CP}C^* > m_P \left(1 + e_{CP}h_{CP}C^* \right)$$

$$\Leftrightarrow C^* \begin{cases} > \frac{m_P}{e_{CP}(\alpha_{CP} - m_Ph_{CP})} & \text{if } m_P < \frac{\alpha_{CP}}{h_{CP}} \\ < \frac{m_P}{e_{CP}(\alpha_{CP} - m_Ph_{CP})} & \text{if } m_P > \frac{\alpha_{CP}}{h_{CP}} \end{cases}$$

But, the case where $m_P > \frac{\alpha_{CP}}{h_{CP}}$ gives us $C^* < 0$, which we cannot have. So, we must restrict ourselves to the case where $m_P < \frac{\alpha_{CP}}{h_{CP}}$. Therefore we have

$$C^* > \frac{m_P}{e_{CP}(\alpha_{CP} - m_P h_{CP})} \quad \text{with } m_P < \frac{\alpha_{CP}}{h_{CP}} \tag{5.3}$$

Since the logistic equation is a supersolution to the consumer equation in subsystem (5.2), we have that $C^* < \left(\frac{r_C - H_C}{r_C}\right) K_C$. Thus, inequality (5.3) implies that

$$K_C > \frac{m_P}{e_{CP}(\alpha_{CP} - m_P h_{CP})} \left(\frac{r_C}{r_C - H_C}\right).$$

This condition requires K_C to be larger than in the case where there is no harvesting, in order to have coexistence.

The stability of the boundary equilibria, when they exist, and the permanence of the system are given by the following theorem.

Theorem 5.1. *If*

(a) $H_C > r_C$ then $(0,0)$ is a stable node.

(b) $H_C < r_C$ then $(0,0)$ is a saddle and $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ is a

    (i) stable node if $H_C > r_C \left(1 - \frac{m_P}{K_C e_{CP}(\alpha_{CP} - h_{CP} m_P)}\right)$.

    (ii) saddle if $H_C < r_C \left(1 - \frac{m_P}{K_C e_{CP}(\alpha_{CP} - h_{CP} m_P)}\right)$. In this case, the system is permanent.

Proof. The eigenvalues of the linearized system at $(0,0)$ are $\lambda_1 = r_C - H_C$ and $\lambda_2 = -m_P$. If $H_C > r_C$ then $\lambda_1 < 0$ and $\lambda_2 < 0$ so $(0,0)$ is a stable node. If $H_C < r_C$ then $\lambda_1 > 0$ and $\lambda_2 < 0$ so $(0,0)$ is a saddle.

The eigenvalues of the linearized system at $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ are

$$\lambda_1 = H_C - r_C$$

$$\lambda_2 = \frac{K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C}{r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP}}.$$

We must have $H_C < r_C$ in order for $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ to be biologically relevant. We see that in this case, $\lambda_1 < 0$. We have that $\lambda_2 > 0$ if either

$$K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C > 0$$

with

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} > 0$$

or

$$K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C < 0$$

with

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} < 0.$$

We have that $\lambda_2 < 0$ if either

$$K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C > 0$$

with

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} < 0$$

or

$$K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C < 0$$

with

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} > 0.$$

Note that

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} > 0 \Leftrightarrow H_C < r_C + \frac{r_C}{K_C e_{CP} h_{CP}}$$

and

$$r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} < 0 \Leftrightarrow H_C > r_C + \frac{r_C}{K_C e_{CP} h_{CP}}.$$

Since we are in the case where $H_C < r_C$, we cannot have $H_C > r_C + \frac{r_C}{K_C e_{CP} h_{CP}}$. So for all biologically relevant situations, we must have $r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} > 0$.

In order to have $K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C > 0$, we must either have

$$H_C > r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right) \text{ if } h_{CP} m_P > \alpha_{CP} \Leftrightarrow m_P > \frac{\alpha_{CP}}{h_{CP}}$$

$$H_C < r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right) \text{ if } h_{CP} m_P < \alpha_{CP} \Leftrightarrow m_P < \frac{\alpha_{CP}}{h_{CP}}$$

In order to have $K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C < 0$, we must either have

$$H_C > r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right) \text{ if } h_{CP} m_P < \alpha_{CP} \Leftrightarrow m_P < \frac{\alpha_{CP}}{h_{CP}}$$

$$H_C < r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right) \text{ if } h_{CP} m_P > \alpha_{CP} \Leftrightarrow m_P > \frac{\alpha_{CP}}{h_{CP}}$$

Since we cannot have $m_P > \frac{\alpha_{CP}}{h_{CP}}$, then we have that $H_C < r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right)$ $\Rightarrow K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C > 0$ and $H_C > r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP} m_P - \alpha_{CP})} \right) \Rightarrow K_C e_{CP} h_{CP} m_P H_C + \alpha_{CP} e_{CP} K_C r_C - m_P e_{CP} h_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C - m_P r_C < 0$.

Thus, we have $\lambda_2 > 0$ when $H_C < r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP}m_P - \alpha_{CP})}\right)$. In this case, $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ is a saddle. But when $H_C > r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP}m_P - \alpha_{CP})}\right)$ then $\lambda_2 < 0$ so $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ is a stable node.

Inequality (3.3) tells us that in order to have permanence in this case, we must have

$$\alpha_{CP}e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C > \left(e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right) K_C + 1\right) m_P$$

$$\Leftrightarrow H_C < r_C \left(1 + \frac{m_P}{K_C e_{CP}(h_{CP}m_P - \alpha_{CP})}\right)$$

which is the same condition we have in order for $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ to be a saddle. $\quad \square$

Biological Remark: This situation presents an interesting result, which we will discuss in section 7.9.

5.1.2 Harvesting only the Predators

In this case, the form of the subsystem is

$$\frac{dC}{dt} = r_C C \left(1 - \frac{C}{K_C}\right) - \frac{e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P}$$

$$\frac{dP}{dt} = \frac{\alpha_{CP}e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P} - (m_P + H_P)P \quad (5.4)$$

There are three possibly biologically relevant equilibria for this subsystem: $(0,0)$, $(K_C, 0)$, and $\left(C^*, P^*\right)$, where

$$C^* = \frac{r_C K_C \alpha_{CP}e_P h_P + (m_P + H_P)K_C e_{CP}h_{CP} - \alpha_{CP}e_{CP}K_C}{2r_C \alpha_{CP}e_P h_P}$$

$$+ \frac{\sqrt{[r_C K_C \alpha_{CP}e_P h_P + (m_P + H_P)K_C e_{CP}h_{CP} - \alpha_{CP}e_{CP}K_C]^2 + 4r_C K_C \alpha_{CP}e_P h_P(m_P + H_P)}}{2r_C \alpha_{CP}e_P h_P}$$

and

$$P^* = \frac{\alpha_{CP}e_{CP}C^* - (m_P + H_P)\left(1 + e_{CP}h_{CP}C^*\right)}{e_P h_P(m_P + H_P)}$$

We always have $C^* > 0$, so for $\left(C^*, P^*\right)$ to be biologically relevant, we must have

$$P^* > 0 \Leftrightarrow \alpha_{CP} e_{CP} C^* > (m_P + H_P)\left(1 + e_{CP} h_{CP} C^*\right)$$

$$\Leftrightarrow C^* \begin{cases} > \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} & \text{if } \alpha_{CP} - (m_P + H_P)h_{CP} > 0 \\[2mm] < \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} & \text{if } \alpha_{CP} - (m_P + H_P)h_{CP} < 0 \end{cases}$$

Clearly we cannot have $\alpha_{CP} - (m_P + H_P)h_{CP} < 0$ because then we would have $C^* < 0$. Thus, we cannot have $H_P > \frac{\alpha_{CP}}{h_{CP}} - m_P$, so we must restrict ourselves to the cases where $H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$. Therefore we have

$$C^* > \frac{m_P + H_P}{e_{CP}\left[\alpha_{CP} - (m_P + H_P)h_{CP}\right]} \tag{5.5}$$

Biological Remark: If $m_P > \frac{\alpha_{CP}}{h_{CP}}$ then we would have $H_P > \frac{\alpha_{CP}}{h_{CP}} - m_P$ for any biologically relevant value of H_P. Thus, if the predators are not sufficiently efficient at gaining from feeding upon the consumers in the absence of harvesting, then the predators cannot survive with any level of harvesting. So we will restrict ourselves to the case where $m_P < \frac{\alpha_{CP}}{h_{CP}}$.

Since the logistic equation is a supersolution to the consumer equation, we have that $C^* < K_C$. Thus, inequality (5.5) implies that

$$K_C > \frac{m_P + H_P}{e_{CP}\left[\alpha_{CP} - (m_P + H_P)h_{CP}\right]}$$
$$\Leftrightarrow H_P < \frac{K_C e_{CP} \alpha_{CP} - K_C e_{CP} h_{CP} m_P - m_P}{K_C e_{CP} h_{CP} + 1}$$
$$\Leftrightarrow H_P < \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C} - m_P \tag{5.6}$$

Note that

$$\frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P = \frac{\alpha_{CP}}{h_{CP}}\left(\frac{e_{CP}K_C}{\frac{1}{h_{CP}}+e_{CP}K_C}\right) - m_P$$

$$< \frac{\alpha_{CP}}{h_{CP}} - m_P$$

So, inequality (5.6) gives us a stricter condition on H_P.

Since we must have $H_P > 0$, we are required to have

$$K_C e_{CP}\alpha_{CP} - K_C e_{CP}h_{CP}m_P - m_P > 0 \Leftrightarrow m_P < \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}.$$

The stability of the boundary equilibria, when they exist, and the permanence of the system are given by the following theorem.

Theorem 5.2. *The equilibrium point $(0,0)$ is a saddle. The equilibrium point $(K_C, 0)$ is a*

(a) stable node if the reverse of inequality (5.6) holds.

(b) saddle if inequality (5.6) holds. In this case, the system is permanent.

Proof. The eigenvalues of the linearized system at $(0,0)$ are $\lambda_1 = r_C > 0$ and $\lambda_2 = -m_P < 0$. Thus, $(0,0)$ is a saddle.

The eigenvalues of the linearized system at $(r_C, 0)$ are $\lambda_1 = -r_C < 0$ and $\lambda_2 = \frac{-e_{CP}h_{CP}K_C(m_P+H_P)+\alpha_{CP}e_{CP}K_C-(m_P+H_P)}{1+e_{CP}h_{CP}K_C}$. We have that

$$\lambda_2 > 0 \Leftrightarrow -e_{CP}h_{CP}K_C(m_P+H_P)+\alpha_{CP}e_{CP}K_C-(m_P+H_P) > 0$$

$$\Leftrightarrow H_P < \frac{e_{CP}K_C(\alpha_{CP}-m_Ph_{CP})-m_P}{1+e_{CP}h_{CP}K_C}$$

$$\Leftrightarrow H_P < \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P$$

and

$$\lambda_2 < 0 \Leftrightarrow -e_{CP}h_{CP}K_C(m_P + H_P) + \alpha_{CP}e_{CP}K_C - (m_P + H_P) < 0$$

$$\Leftrightarrow H_P > \frac{e_{CP}K_C(\alpha_{CP} - m_P h_{CP}) - m_P}{1 + e_{CP}h_{CP}K_C}$$

$$\Leftrightarrow H_P > \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C} - m_P$$

Thus, $(K_C, 0)$ will be a saddle when $H_P < \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P$ and a stable node when $H_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P$.

Inequality (3.3) tells us that in order to have permanence in this case, we must have

$$\alpha_{CP}e_{CP}K_C > (e_{CP}h_{CP}K_C + 1)(m_P + H_P) \Leftrightarrow H_P < \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C} - m_P$$

which is exactly inequality (5.6). □

Remarks:

(i) If $m_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$ then we are guaranteed to have $H_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P$ since $H_P > 0$. But $m_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$ is the reverse of condition (3.7). Thus, if the predators cannot survive in the system where there is no harvesting, then they cannot survive with any level of harvesting.

(ii) We have that $(K_C, 0)$ is a saddle if $H_P < \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P \Leftrightarrow m_P < \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - H_P$ and a stable node if $H_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - m_P \Leftrightarrow m_P > \frac{\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} - H_P$. Thus, it is harder for the consumer and predator to coexist in this case than in the case where there is no harvesting. Similarly, it is easier for the predator to be excluded from the system in this case than in the case where there is no harvesting.

5.1.3 Harvesting Both the Consumers and Predators

In this case, the form of the subsystem is

$$\frac{dC}{dt} = (r_C - H_C)\left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right)K_C}\right) - \frac{e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P}$$

$$\frac{dP}{dt} = \frac{\alpha_{CP}e_{CP}CP}{1 + e_{CP}h_{CP}C + e_P h_P P} - (m_P + H_P)P \tag{5.7}$$

There are three possibly biologically relevant equilibria for this subsystem: $(0,0)$, $\left(\left(\frac{r_C - H_C}{r_C}\right)K_C, 0\right)$, and (C^*, P^*), where

$$C^* = \frac{\frac{(r_C - H_C)^2}{r_C}K_C\alpha_{CP}e_P h_P + e_{CP}h_{CP}(m_P + H_P)\left(\frac{r_C - H_C}{r_C}\right)K_C - \alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C}{2(r_C - H_C)\alpha_{CP}e_P h_P}$$

$$+ \frac{1}{2(r_C - H_C)\alpha_{CP}e_P h_P}\left(\left[\frac{(r_C - H_C)^2}{r_C}K_C\alpha_{CP}e_P h_P + e_{CP}h_{CP}(m_P + H_P)\left(\frac{r_C - H_C}{r_C}\right)K_C\right.\right.$$

$$\left.\left. - \alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right]^2 + 4\alpha_{CP}e_P h_P(m_P + H_P)\frac{(r_C - H_C)^2}{r_C}K_C\right)^{1/2}$$

and

$$P^* = \frac{\alpha_{CP}e_{CP}C^* - (m_P + H_P)\left(1 + e_{CP}h_{CP}C^*\right)}{e_P h_P(m_P + H_P)}.$$

Note that in order for $\left(\left(\frac{r_C - H_C}{r_C}\right)K_C, 0\right)$ to be biologically relevant, we must have $H_C < r_C$ and in order for (C^*, P^*) to be biologically relevant, we must have

$$P^* > 0 \Leftrightarrow \alpha_{CP}e_{CP}C^* > (m_P + H_P)\left(1 + e_{CP}h_{CP}C^*\right)$$

$$\Leftrightarrow C^* \begin{cases} > \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} & \text{if } \alpha_{CP} - (m_P + H_P)h_{CP} > 0 \\ < \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} & \text{if } \alpha_{CP} - (m_P + H_P)h_{CP} < 0 \end{cases}$$

Clearly we cannot have $\alpha_{CP} - (m_P + H_P)h_{CP} < 0$ because then we would have $C^* < 0$. Thus, we must have $H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$. Since H_P must be positive, we are required to

have $m_P < \frac{\alpha_{CP}}{h_{CP}}$. Therefore, we have

$$C^* > \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \tag{5.8}$$

Since the logistic equation is a supersolution to the consumer equation, we have that $C^* < \left(\frac{r_C - H_C}{r_C}\right) K_C$. Thus, inequality (5.8) implies that

$$K_C > \frac{m_P + H_P}{e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \left(\frac{r_C}{r_C - H_C}\right)$$

$$\Leftrightarrow H_C < r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]}\right)$$

$$\Leftrightarrow H_P < \frac{\left(\frac{r_C - H_C}{r_C}\right) K_C e_{CP}}{\left(\frac{r_C - H_C}{r_C}\right) K_C e_{CP} h_{CP} + m_P} \left(\frac{\alpha_{CP}}{h_{CP}} - m_P\right)$$

$$- \frac{m_P}{\left(\frac{r_C - H_C}{r_C}\right) K_C e_{CP} h_{CP} + m_P}.$$

Remarks:

1. If $H_C < r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]}\right)$ then $H_C < \frac{\alpha_{CP}}{h_{CP}} - m_P$. So, if $\left(C^*, P^*\right)$ is biologically relevant, then $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ will also be biologically relevant.

2. Since we must have $H_C > 0$, it is necessary to have $H_P < \frac{K_C e_{CP}}{K_C e_{CP} h_{CP} + m_P} \left(\frac{\alpha_{CP}}{h_{CP}} - m_P\right) - \frac{m_P}{K_C e_{CP} h_{CP} + m_P}$, which requires us to have $m_P < \frac{K_C \alpha_{CP} e_{CP}}{1 + K_C e_{CP} h_{CP}}$. Since we must have $H_P > 0$, it is necessary to have $H_C < r_C \left(1 - \frac{m_P}{K_C e_{CP}(\alpha_{CP} - h_{CP} m_P)}\right)$, which also requires us to have $m_P < \frac{K_C \alpha_{CP} e_{CP}}{1 + K_C e_{CP} h_{CP}}$.

The stability of the boundary equilibria, when they exist, and permanence of the system are given by the following theorem.

Theorem 5.3. *If*

(a) $H_C > r_C$ *then* $(0, 0)$ *is a stable node.*

(b) $H_C < r_C$ *then* $(0, 0)$ *is a saddle and* $\left(\left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ *is a*

(i) *stable node if* $H_C > r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$.

(ii) *saddle if* $H_C < r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$. *In this case, the system is permanent.*

Proof. The eigenvalues of the linearized system at $(0,0)$ are $\lambda_1 = r_C - H_C$ and $\lambda_2 = -(m_P + H_P) < 0$. If $H_C > r_C$ then $\lambda_1 < 0$ and $\lambda_2 < 0$ so $(0,0)$ is a stable node. If $H_C < r_C$ then $\lambda_1 > 0$ and $\lambda_2 < 0$ so $(0,0)$ is a saddle. In this case, $\left(\left(\frac{r_C-H_C}{r_C}\right)K_C, 0\right)$ is biologically relevant.

The eigenvalues of the linearized system at $\left(\left(\frac{r_C-H_C}{r_C}\right)K_C, 0\right)$ are

$$\lambda_1 = H_C - r_C$$

$$\lambda_2 = m_P + h_P + \frac{\alpha_{CP} e_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C}{r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP}}.$$

Since we are in the case where $H_C < r_C$, we have $\lambda_1 > 0$. We also have that $r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP} > r_C + r_C K_C e_{CP} h_{CP} - r_C K_C e_{CP} h_{CP} = r_C > 0$. Thus, the sign of λ_2 is determined by the sign of $(m_P + H_P)(r_C + r_C K_C e_{CP} h_{CP} - H_C K_C e_{CP} h_{CP}) + \alpha_{CP} e_{CP} K_C r_C - K_C e_{CP} \alpha_{CP} H_C$, which for the moment we will define as β.

In order to have $\beta > 0$, we must either have

$$H_C > r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]}\right) \text{ if } H_P > \frac{\alpha_{CP}}{h_{CP}} - m_P$$

$$H_C < r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]}\right) \text{ if } H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$$

Since we are in the case where $H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$, then we we will have $\beta > 0$ if and only if $H_C < r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$. Similarly, in order to have $\beta < 0$, we must have $H_C > r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$.

So, if $H_C < r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$ then $\lambda_2 > 0$ so $\left(\left(\frac{r_C-H_C}{r_C}\right)K_C, 0\right)$ is a saddle. And if $H_C > r_C \left(1 - \frac{m_P+H_P}{K_C e_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$ then $\left(\left(\frac{r_C-H_C}{r_C}\right)K_C, 0\right)$ is a

stable node.

Inequality (3.3) tells us that in order to have permanence in this case, we must have

$$\alpha_{CP}e_{CP}\left(\tfrac{r_C-H_C}{r_C}\right)K_C > \left(e_{CP}h_{CP}\left(\tfrac{r_c-H_c}{r_C}\right)K_C + 1\right)(m_P + H_P)$$

$$\Leftrightarrow H_C < r_C\left(1 - \tfrac{m_P+H_P}{K_Ce_{CP}[\alpha_{CP}-(m_P+H_P)h_{CP}]}\right)$$

which is the same condition we have in order for $\left(\left(\tfrac{r_C-H_C}{r_C}\right)K_C, 0\right)$ to be a saddle. $\square$

Biological Remark: This situation presents an interesting result, which we will discuss in section 7.9.

5.2   Harvesting the $R-P$ Subsystem

5.2.1   Harvesting only the Resource

In this case, the form of the subsystem is

$$\frac{dR}{dt} = (r_R - H_R)R\left(1 - \frac{R}{\left(\tfrac{r_R-H_R}{r_R}\right)K_R}\right) - \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_Ph_PP}$$

$$\frac{dP}{dt} = \frac{\alpha_{RP}e_{RP}RP}{1 + e_{RP}h_{RP}R + e_Ph_PP} - m_PP \tag{5.9}$$

Note that the form of subsystem (5.9) is the same as subsystem (5.2). So the results from Section 5.1 hold equally well in this section, but with C now replaced by R. In particular, there are three possibly biologically relevant equilibria for this subsystem: $(0,0)$, $\left(\left(\tfrac{r_R-H_R}{r_R}\right)K_R, 0\right)$, and (R^*, P^*), where

$$R^* = \frac{\beta + \sqrt{\beta^2 + 4\alpha_{RP}e_Ph_Pm_P\left(\tfrac{(r_R-H_R)^2}{r_R}\right)K_R}}{2(r_R - H_R)\alpha_{RP}e_Ph_P}$$

for

$$\beta = \frac{(r_R - H_R)^2}{r_R} K_R \alpha_{RP} e_P h_P + e_{RP} h_{RP} m_P \left(\frac{r_R - H_R}{r_R}\right) K_R - \alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R$$

and

$$P^* = \frac{\alpha_{RP} e_{RP} R^* - m_P \left(1 + e_{RP} h_{RP} R^*\right)}{e_P h_P m_P}$$

In order for $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ to be biologically relevant, we must have $H_R < r_R$ and in order for (R^*, P^*) to be biologically relevant, we must have

$$R^* > \frac{m_P}{e_{RP}(\alpha_{RP} - m_P h_{RP})} \quad \text{with } m_P < \frac{\alpha_{RP}}{h_{RP}} \tag{5.10}$$

Since the logistic equation is a supersolution to the resource equation in (5.9), we have that $R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$. Thus, inequality (5.10) implies that

$$K_R > \frac{m_P}{e_{RP}(\alpha_{RP} - m_P h_{RP})} \left(\frac{r_R - H_R}{r_R}\right).$$

This conditions requires K_R to be larger than in the case where there is no harvesting, in order to have coexistence.

The stability of these equilibria, when they exist, and permanence of the system are given by the following.

Theorem 5.4. *If*

(a) $H_R > r_R$ *then* $(0,0)$ *is a stable node.*

(b) $H_R < r_R$ *then* $(0,0)$ *is a saddle and* $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ *is a*

    (i) *stable node if* $H_R > r_R \left(1 \frac{m_P}{K_R e_{RP}(\alpha_{RP} - h_{RP} m_P)}\right).$

    (ii) *saddle if* $H_R < r_R \left(1 - \frac{m_P}{K_R e_{RP}(\alpha_{RP} - h_{RP} m_P)}\right).$

The proof is identical to the proof of Theorem 5.1.

Biological Remark: If $r_R \left(1 \frac{m_P}{K_R e_{RP}(\alpha_{RP} - h_{RP} m_P)}\right) < H_R < r_R$ then the resource can survive, while the predators go extinct. Thus, if the consumers are harvested at a sufficiently high rate, there will be not be enough food to sustain the predators.

5.2.2 Harvesting only the Predators

In this case, the form of the subsystem is

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P}$$

$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P} - (m_P + H_P) P \qquad (5.11)$$

Note that the form of subsystem (5.11) is the same as subsystem (5.4). So the results from Section 5.1 hold equally well in this section, but with C now replaced by R. In particular, there are three possibly biologically relevant equilibria for this subsystem: $(0, 0)$, $(K_R, 0)$, and $\left(R^*, P^*\right)$, where

$$R^* = \frac{r_R K_R \alpha_{RP} e_P h_P + (m_P + H_P) K_R e_{RP} h_{RP} - \alpha_{RP} e_{RP} K_R}{2 r_R \alpha_{RP} e_P h_P}$$

$$+ \frac{\sqrt{[r_R K_R \alpha_{RP} e_P h_P + (m_P + H_P) K_R e_{RP} e_P h_P - \alpha_{RP} e_{RP} K_R]^2 + 4 r_R K_R \alpha_{RP} e_P h_P (m_P + H_P)}}{2 r_R \alpha_{RP} e_P h_P}$$

and

$$P^* = \frac{\alpha_{RP} e_{RP} R^* - (m_P + H_P)\left(1 + e_{RP} h_{RP} R^*\right)}{e_P h_P (m_P + H_P)}$$

We always have $R^* > 0$, so for $\left(R^*, P^*\right)$ to be biologically relevant, we must have

$$R^* > \frac{m_P + H_P}{e_{RP}\left[\alpha_{RP}(m_P + H_P) h_{RP}\right]} \quad \text{if } \alpha_{RP} - (m_P + H_P) h_{RP} > 0 \qquad (5.12)$$

Since the logistic equation is a supersolution to the resource equation, we have that $R^* < K_R$. Thus, inequality (5.12) implies that

$$H_P < \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R} - m_P. \qquad (5.13)$$

So, inequality (5.13) gives us a stricter condition on H_P than $H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$.

The stability of the boundary equilibria are given by the following theorem.

Theorem 5.5. *The equilibrium point $(0,0)$ is a saddle. The equilibrium point $(K_R, 0)$ is a*

(a) *saddle if $H_P < \frac{e_{RP}K_R(\alpha_{RP} - m_P h_{RP}) - m_P}{1 + e_{RP}h_{RP}K_R}$.*

(b) *stable node if $H_P > \frac{e_{RP}K_R(\alpha_{RP} - m_P h_{RP}) - m_P}{1 + e_{RP}h_{RP}K_R}$.*

The proof of the theorem is identical to the proof of theorem 5.2.

Remarks:

(i) If $m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R}$ then we are guaranteed to have $H_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R} - m_P$ since $H_P > 0$. But $m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R}$ is the reverse of condition (3.3). Thus, if the predators cannot survive in the system where there is no harvesting, then they cannot survive with any level of harvesting.

(ii) We have that $(K_R, 0)$ is a saddle if $H_P < \frac{e_{RP}K_R(\alpha_{RP} - m_P h_{RP}) - m_P}{1 + e_{RP}h_{RP}K_R} \Leftrightarrow m_P < \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R} - H_P$ and a stable node if $H_P > \frac{e_{RP}K_R(\alpha_{RP} - m_P h_{RP}) - m_P}{1 + e_{RP}h_{RP}K_R} \Leftrightarrow m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R} - H_P$. Thus, it is harder for the resource and predator to coexist in this case than in the case where there is no harvesting. Similarly, it is easier for the predator to be excluded from the system in this case than in the case where there is no harvesting.

5.2.3   Harvesting Both the Resource and Predators

In this case, the form of the subsystem is

$$
\begin{aligned}
\frac{dR}{dt} &= (r_R - H_R)\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_P h_P P} \\
\frac{dP}{dt} &= \frac{\alpha_{RP}e_{RP}RP}{1 + e_{RP}h_{RP}R + e_P h_P P} - (m_P + H_P)P
\end{aligned}
\tag{5.14}
$$

Note that the form of subsystem (5.14) is as subsystem (5.7). So the results from Section 5.1.3 hold equally well in this section, but with C replaced by R. In particular, there are three possibly biologically relevant equilibria for this subsystem: $(0,0)$, $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$, and $\left(R^*, P^*\right)$, where

$$
R^* = \frac{\frac{(r_R - H_R)^2}{r_R} K_R \alpha_{RP} e_P h_P + e_{RP} h_{RP}(m_P + H_P)\left(\frac{r_R - H_R}{r_R}\right) K_R - \alpha_{RP} e_{RP}\left(\frac{r_R - H_R}{r_R}\right) K_R}{2(r_R - H_R)\alpha_{RP} e_P h_P}
$$

$$
+ \frac{1}{2(r_R - H_R)\alpha_{RP} e_P h_P}\left(\left[\frac{(r_R - H_R)^2}{r_R} K_R \alpha_{RP} e_P h_P + e_{RP} h_{RP}(m_P + H_P)\left(\frac{r_R - H_R}{r_R}\right) K_R\right.\right.
$$

$$
\left.\left. - \alpha_{RP} e_{RP}\left(\frac{r_R - H_R}{r_R}\right) K_R\right]^2 + 4\alpha_{RP} e_P h_P(m_P + H_P)\frac{(r_R - H_R)^2}{r_R} K_R\right)^{1/2}
$$

and

$$
P^* = \frac{\alpha_{RP} e_{RP} R^* - (m_P + H_P)\left(1 + e_{RP} h_{RP} R^*\right)}{e_P h_P(m_P + H_P)}.
$$

In order for $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ to be biologically relevant, we must have $H_R < r_R$ and in order for $\left(R^*, P^*\right)$ to be biologically relevant, we must have

$$
R^* > \frac{m_P + H_P}{e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]} \quad \text{with } \alpha_{RP} - (m_P + H_P)h_{RP} > 0 \tag{5.15}
$$

Since we cannot have $R^* < 0$, we must have $H_P < \frac{\alpha_{RP}}{h_{RP}} - m_P$. Since H_P must be positive, we are required to have $m_P < \frac{\alpha_{RP}}{h_{RP}}$.

Since the logistic equation is a supersolution to the resource equation, we have that $R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$. Thus, inequality (5.15) implies that

$$
K_R > \frac{m_P + H_P}{e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]}\left(\frac{r_R}{r_R - H_R}\right).
$$

This condition requires K_R to be larger than in the case where only the predators are

being harvested. This condition is equivalent to

$$H_R < r_R \left(1 - \frac{m_P + H_P}{K_R e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]}\right)$$

or

$$H_P < \frac{\left(\frac{r_R - H_R}{r_R}\right) K_R e_{RP}}{\left(\frac{r_R - H_R}{r_R}\right) K_R e_{RP} h_{RP} + m_P} \left(\frac{\alpha_{RP}}{h_{RP}} - m_P\right) - \frac{m_P}{\left(\frac{r_R - H_R}{r_R}\right) K_R e_{RP} h_{RP} + m_P}.$$

Remarks:

1. If $H_R < r_R \left(1 - \frac{m_P + H_P}{K_R e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]}\right)$ then $H_R < \frac{\alpha_{RP}}{h_{RP}} - m_P$. So, if $\left(R^*, P^*\right)$ is biologically relevant, then $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ will also be biologically relevant.

2. Since we must have $H_R > 0$, it is necessary to have $H_P < \frac{K_R e_{RP}}{K_R e_{RP} h_{RP} + m_P} \left(\frac{\alpha_{RP}}{h_{RP}} - m_P\right) - \frac{m_P}{K_R e_{RP} h_{RP} + m_P}$, which requires us to have $m_P < \frac{K_R \alpha_{RP} e_{RP}}{1 + K_R e_{RP} h_{RP}}$. Since we must have $H_P > 0$, it is necessary to have $H_R < r_R \left(1 - \frac{m_P}{K_R e_{RP}(\alpha_{RP} - h_{RP} m_P)}\right)$, which also requires us to have $m_P < \frac{K_R \alpha_{RP} e_{RP}}{1 + K_R e_{RP} h_{RP}}$.

The stability of the boundary equilibria, when they exist, and the permanence of the system are given by the following theorem.

Theorem 5.6. *If*

(a) $H_R > r_R$ *then* $(0, 0)$ *is a stable node.*

(b) $H_R < r_R$ *then* $(0, 0)$ *is a saddle and* $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ *is a*

   (i) stable node if $H_R > r_R \left(1 - \frac{m_P + H_P}{K_R e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]}\right)$.

   (ii) saddle if $H_R < r_R \left(1 - \frac{m_P + H_P}{K_R e_{RP}[\alpha_{RP} - (m_P + H_P)h_{RP}]}\right)$. *In this case, the system is permanent.*

The proof is identical to the proof of Theorem 5.3.

Biological Remark: We have that

$$
\begin{cases}
H_P < \frac{\alpha_{RP}}{h_{RP}} - m_P \\
H_R < r_C\left(1 - \frac{m_P+H_P}{K_R e_{CP}[\alpha_{RP}-(m_P+H_P)h_{RP}]}\right)
\end{cases}
\Leftrightarrow
\begin{cases}
H_P < \frac{\alpha_{RP}}{h_{RP}}\left(\frac{e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{\frac{1}{h_{RP}}+e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}\right) - m_P \\
H_R < r_R
\end{cases}
$$

But $r_R\left(1 - \frac{m_P+H_P}{K_C e_{RP}[\alpha_{RP}-(m_P+H_P)h_{RP}]}\right) < r_R$ and $\frac{\alpha_{RP}}{h_{RP}}\left(\frac{e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{\frac{1}{h_{RP}}+e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}\right) - m_P <$ $\frac{\alpha_{RP}}{h_{RP}} - m_P$. So there is a tradeoff in the amount of harvesting that can be done on each species. If $H_R > r_R\left(1 - \frac{m_P+H_P}{K_R e_{RP}[\alpha_{RP}-(m_P+H_P)h_{RP}]}\right)$ then the maximum value of H_P must be smaller than the case where $H_R < r_R\left(1 - \frac{m_P+H_P}{K_R e_{RP}[\alpha_{RP}-(m_P+H_P)h_{RP}]}\right)$. Similarly, if $H_P > \frac{\alpha_{RP}}{h_{RP}}\left(\frac{e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{\frac{1}{h_{RP}}+e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}\right) - m_P$ then the maximum value of H_R must be smaller than the case where $H_P < \frac{\alpha_{RP}}{h_{RP}}\left(\frac{e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{\frac{1}{h_{RP}}+e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}\right) - m_P$. Biologically this is telling us that if we have a sufficiently large amount of harvesting on the resource, then we must have less harvesting on the predators. Conversely, if we have a sufficiently large amount of harvesting on the predators, then we must have less harvesting on the resource. The reason for this is that harvesting the resource reduces the amount of food available to the predators. If the predators' food supply is shrinking because the resource is being harvested more, then the predators cannot withstand being harvested as much. Similarly, if the predators are being harvested more, they need more food to help sustain themselves so the resource cannot be harvested as much.

5.3 Harvesting the $R - C$ Subsystem

5.3.1 Harvesting only the Resource

In this case, the form of the subsystem is

$$\frac{dR}{dt} = (r_R - H_R)R\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C}$$

$$\frac{dC}{dt} = r_C C\left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C} \qquad (5.16)$$

The possibly biologically relevant equilibria for this subsystem are $(0,0)$, $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$, $(0, K_C)$, and (R^*, C^*), where R^* and C^* are positive solutions to the system

$$0 = (r_R - H_R)\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}C}{1 + e_{RC}h_{RC}R + e_C h_C C}$$

$$0 = r_C\left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC}e_{RC}R}{1 + e_{RC}h_{RC}R + e_C h_C C}$$

Note that in order for $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$ to be biologically relevant, we must have $H_R < r_R$.

The invasibility and exclusion of the resource and consumer species, along with the permanence of the system, are given by the following theorem.

Theorem 5.7. *The consumers can always invade the system at $(0,0)$. The consumers can always invade the system at $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$, when it is biologically relevant.*

(a) If $H_R > r_R$ then the resource will be excluded from the system at $(0,0)$. If $H_R > r_R$ or $r_R < \frac{e_{RC}K_C}{1 + e_C h_C K_C}$ then the resource will be excluded from the system at $(0, K_C)$.

(b) $H_R < r_R$ then the resource can invade the system at $(0,0)$. If we further have that $H_R < r_R - \frac{e_{RC}K_C}{1 + e_C h_C K_C}$ and $r_R > \frac{e_{RC}K_C}{1 + e_C h_C K_C}$, then the resource can invade the

system at $(0, K_C)$.

In the case where the resource can invade the system at $(0, K_C)$, the system is permanent.

Proof. The linearized resource equation at $(0,0)$ is

$$\frac{dR}{dt} = (r_R - H_R)R.$$

If $H_R < r_R$ then the resource's intrinsic growth rate is positive, so the resource can invade the system at $(0,0)$. But if $H_R < r_R$ then the resource's intrinsic growth rate is negative, so the resource is excluded from the system at $(0,0)$.

The linearized consumer equation at $(0,0)$ is

$$\frac{dC}{dt} = r_C C.$$

Since the consumers' intrinsic growth rate is positive, the consumer can invade the system at $(0,0)$.

The linearized resource equation at $(0, K_C)$ is

$$\frac{dR}{dt} = \left(r_R - H_R - \frac{e_{RC} K_C}{1 + e_C h_C K_C} \right) R.$$

If $r_R - \frac{e_{RC} K_C}{1+e_C h_C K_C} < 0$ then $r_R - H_R - \frac{e_{RC} K_C}{1+e_C h_C K_C} < 0$. In this case, the resource's intrinsic growth rate is negative so the resource is excluded from the system at $(0, K_C)$. If

$$H_R < r_R - \frac{e_{RC} K_C}{1 + e_C h_C K_C} \tag{5.17}$$

and $r_R - \frac{e_{RC} K_C}{1+e_C h_C K_C} > 0$ then the resource's intrinsic growth rate is positive, so the resource can invade the system at $(0, K_C)$.

The linearized consumer equation at $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$ is

$$\frac{dC}{dt} = \left(r_C + \frac{\alpha_{RC}e_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R}{1 + e_{RC}h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R}\right)C.$$

Since we must have $H_R < r_R$ in order for this equilibrium to be biologically relevant, we have that the consumers' intrinsic growth rate is positive so the consumers can invade the system at $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$.

In the case where there is no harvesting, permanence condition (3.33) is, in dimensionalized terms, $\frac{e_{RC}K_C}{r_R} < 1 + e_C h_C K_C$. In this case, it becomes $\frac{e_{RC}K_C}{r_R - H_R} < 1 + e_C h_C K_C \Leftrightarrow H_R < r_R - \frac{e_{RC}K_C}{1 + e_C h_C K_C}$. But this is the same as the condition (5.17), which was the condition needed for the resource to be able to invade the system at $(0, K_C)$. $\qquad\square$

Remark: If $r_R < \frac{e_{RC}K_C}{1 + e_C h_C K_C}$ then we cannot have $H_R < r_R - \frac{e_{RC}K_C}{1 + e_C h_C K_C}$ since we must have $H_R > 0$. So if the resource's intrinsic growth rate is not sufficiently large then no matter how little harvesting is done to the resource, the resource still will not be able to invade the system at $(0, K_C)$ and the system still will not be permanent. Thus, the condition for permanence in the system without harvesting of the resource is a necessary but not sufficient condition for permanence in the case where the resource is harvested.

5.3.2 Harvesting only the Consumers

In this case, the form of the subsystem is

$$\begin{aligned}
\frac{dR}{dt} &= r_R R\left(1 - \frac{R}{K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C} \\
\frac{dC}{dt} &= (r_C - H_C)C\left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right)K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C}
\end{aligned} \qquad (5.18)$$

The possibly biologically relevant equilibria for this subsystem are $(0,0)$, $(K_R, 0)$, $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$, and (R^*, C^*), where R^* and C^* are positive solutions to the system

$$0 = r_R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RC} C}{1 + e_{RC} h_{RC} R + e_C h_C C}$$

$$0 = (r_C - H_C) \left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right) K_C}\right) + \frac{\alpha_{RC} e_{RC} R}{1 + e_{RC} h_{RC} R + e_C h_C C}$$

Note that in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ to be biologically relevant, we must have $H_C < r_C$.

The invasibility and exclusion of the resource and consumer species, along with the permanence of the system, are given by the following theorem.

Theorem 5.8. *The resource can always invade the system at* $(0,0)$*. If*

(a) $H_C < r_C$ *then the consumers can invade the system at* $(0,0)$*. Otherwise, the consumers will be excluded from the system at* $(0,0)$*.*

(b) $H_C < r_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$ *then the consumers can invade the system at* $(K_R, 0)$*. Otherwise, the consumers will be excluded from the system at* $(K_R, 0)$*.*

(c) *either* $e_{RC} < r_R e_C h_C$ *or* $e_{RC} > r_R e_C h_C$ *with* $H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$ *then the resource can invade the system at* $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$*. If* $e_{RC} > r_R e_C h_C$ *with* $H_C < r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$ *then the resource is excluded from the system at* $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$*.*

In the cases where the resource can invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ *and the consumers can invade the system at* $(K_R, 0)$*, the system is permanent.*

Proof. The linearized resource equation at $(0,0)$ is

$$\frac{dR}{dt} = r_R R.$$

Since the resource's intrinsic growth rate is positive, the resource can invade the system at $(0,0)$.

The linearized consumer equation at $(0,0)$ is

$$\frac{dC}{dt} = (r_C - H_C)C.$$

If $H_C < r_C$ then the consumers' intrinsic growth rate is positive so the consumers can invade the system at $(0,0)$. But if $H_C > r_C$ then the consumers' intrinsic growth rate is negative so the consumers are excluded from the system at $(0,0)$.

The linearized consumer equation at $(K_R, 0)$ is

$$\frac{dC}{dt} = \left(r_C - H_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}\right)C.$$

If $H_C < r_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$ then the consumers' intrinsic growth rate is positive so the consumers can invade the system at $(K_R, 0)$. But if $H_C > r_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$ then the consumers' intrinsic growth rate is negative so the consumers are excluded from the system at $(K_R, 0)$.

The linearized resource equation at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ is

$$\frac{dR}{dt} = \left(r_R - \frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right) K_C}\right)R.$$

Suppose that $e_{RC} < r_R e_C h_C$. Then the resource's intrinsic growth rate will be positive if $H_C < r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$ and negative if $H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$. But, in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ to be biologically relevant, we must have $H_C < r_C$. Thus, we cannot have $H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$ since $r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) > r_C$, which would give us $H_C > r_C$. Thus, if $e_{RC} < r_R e_C h_C$ then the resource's intrinsic growth rate will always be positive so the resource will be able to invade the system

at $\left(0, \left(\frac{r_C - H_C}{r_C}\right)\right)$.

Suppose now that $e_{RC} > r_R e_C h_C$. Then the resource's intrinsic growth rate will be positive if

$$H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right). \tag{5.19}$$

In this case, the resource will be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$. And the resource's intrinsic growth rate will be negative if $H_C < r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right)$. In this case, the resource will be excluded from the system.

Taking the dimensionalized form of permanence condition (3.33), which is when there is no harvesting, gives us the permanence condition in the case where the consumers are being harvested. In particular, the permanence condition becomes $\frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right) K_C}{r_R} < e_C h_C \left(\frac{r_C - H_C}{r_C}\right) K_C + 1$, which is equivalent to condition (5.19), which is the condition needed for the resource's intrinsic growth rate to be positive at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$.

Note that in the case where there was no harvesting, the consumers were always able to invade the system at $(K_R, 0)$. But now, we do not have the same guarantee if H_C is too big. Thus, if the consumers are able to invade at $(K_R, 0)$ then we will have permanence. $\qquad \square$

Biological Remark: This situation presents an interesting result, which we will discuss in section 7.9.

5.3.3 Harvesting Both the Resource and Consumers

In this case, the form of the subsystem is

$$\frac{dR}{dt} = (r_R - H_R)R\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_Ch_CC}$$

$$\frac{dC}{dt} = (r_C - H_C)C\left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right)K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_Ch_CC} \qquad (5.20)$$

The possibly biologically relevant equilibria for this subsystem are $(0,0)$, $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$, $\left(0, \left(\frac{r_C - H_C}{r_C}\right)K_C\right)$, and (R^*, C^*), where R^* and C^* are positive solutions to the system

$$0 = (r_R - H_R)\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}C}{1 + e_{RC}h_{RC}R + e_Ch_CC}$$

$$0 = (r_C - H_C)\left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right)K_C}\right) + \frac{\alpha_{RC}e_{RC}R}{1 + e_{RC}h_{RC}R + e_Ch_CC}$$

Note that in order for $\left(0, \left(\frac{r_R - H_R}{r_R}\right)K_R\right)$ to be biologically relevant, we must have $H_R < r_R$, and in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right)K_C\right)$ to be biologically relevant, we must have $H_C < r_C$.

The invasibility and exclusion of the resource and consumer species are given by the following theorem.

Theorem 5.9. *If*

(a) $H_R < r_R$ then the resource can invade the system at $(0,0)$, and $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$ is biologically relevant. If $H_R < r_R$ with $H_C < r_C + \frac{\alpha_{RC}e_{RC}(r_R - H_R)K_R}{r_R + e_{RC}h_{RC}(r_R - H_R)K_R}$ or if $H_C < \frac{\alpha_{RC}}{h_{RC}} + r_C$ with $H_R < r_R\left(1 - \frac{H_C - r_C}{e_{RC}K_R[\alpha_{RC} - (H_C - r_C)h_{RC}]}\right)$, then the consumers can invade the system at $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$. If $H_C < r_C$ then the consumers can invade the system for any level H_R of harvesting on the resource.

(b) $H_C < r_C$ then the consumers can invade the system at $(0,0)$ and $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ is biologically relevant. If $e_{RC} < r_R e_C h_C$ and $H_R < r_R - \frac{e_{RC}}{e_C h_C}$ then the resource can invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C} K_C\right)\right)$ for any level of consumers harvesting, H_C. If $H_C > r_C \left(1 + \frac{r_R - H_R}{K_C[e_C h_C(r_R - H_R) - e_{RC}]}\right)$ with either $e_{RC} > r_R e_C h_C$ and $H_R < r_R$, or $e_{RC} < r_R e_C h_C$ and $r_R - \frac{e_{RC}}{e_C h_C} < H_R < r_R$, then the resource can invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$.

Proof. The linearized resource equation at $(0,0)$ is

$$\frac{dR}{dt} = (r_R - H_R)R.$$

If $H_R < r_R$ then the resource's intrinsic growth rate is positive so the resource can invade the system at $(0,0)$. If $H_R > r_R$ then the resource's intrinsic growth rate is negative so the resource is excluded from the system at $(0,0)$.

The linearized consumer equation at $(0,0)$ is

$$\frac{dC}{dt} = (r_C - H_C)C.$$

If $H_C < r_C$ then the consumers' intrinsic growth rate is positive so the consumers can invade the system at $(0,0)$. If $H_C < r_C$ then the consumers' intrinsic growth rate is negative so the consumers are excluded from the system at $(0,0)$.

If $H_R < r_R$, then the linearized consumer equation at $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$ is

$$\frac{dC}{dt} = \left(r_C - H_C + \frac{\alpha_{RC} e_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}\right) C.$$

The consumers' intrinsic growth rate will be positive if $H_C < r_C + \frac{\alpha_{RC} e_{RC}(r_R - H_R)K_R}{r_R + e_{RC} h_{RC}(r_R - H_R)K_R}$.

This is equivalent to having

$$H_R > r_R \left(1 + \frac{H_C - r_C}{e_{RC}K_R[(H_C - r_C)h_{RC} - \alpha_{RC}]}\right) \quad \text{if } H_C > \frac{\alpha_{RC}}{h_{RC}} + r_C \qquad (5.21)$$

$$H_R < r_R \left(1 + \frac{H_C - r_C}{e_{RC}K_R[(H_C - r_C)h_{RC} - \alpha_{RC}]}\right) \quad \text{if } H_C < \frac{\alpha_{RC}}{h_{RC}} + r_C \qquad (5.22)$$

Inequality (5.21) would give us $H_R > r_R$. This contradicts the condition needed for the equilibrium $\left(\left(\frac{r_R - H_R}{r_R}\right)K_R, 0\right)$ to be biologically relevant; namely that $H_R < r_R$. So, we need $H_R < r_R \left(1 + \frac{H_C - r_C}{e_{RC}K_R[(H_C - r_C)h_{RC} - \alpha_{RC}]}\right)$ if $H_C < \frac{\alpha_{RC}}{h_{RC}} + r_C$ in order to have the consumers' intrinsic growth rate be positive. Note that if $H_C < r_C$, then the condition that $H_R < r_R$ implies (5.22).

If $H_C < r_C$, then the linearized resource equation at $\left(0, \left(\frac{r_C - H_C}{r_C}\right)K_C\right)$ is

$$\frac{dR}{dt} = \left(r_R - H_R - \frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right)K_C}\right)R.$$

The resource's intrinsic growth rate is positive if $H_R < r_R - \frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right)K_C}$. Note that in order to have $H_R > 0$, we must have

$$H_C < r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) \quad \text{if } r_R e_C h_C > e_{RC}$$

$$H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) \quad \text{if } r_R e_C h_C < e_{RC}$$

Having $H_R < r_R - \frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right)K_C}$ is equivalent to

$$H_C < r_C \left(1 + \frac{r_R - H_R}{K_C[(r_R - H_R)e_C h_C - e_{RC}]}\right) \quad \text{if } H_R < r_R - \frac{e_{RC}}{e_C h_C} \qquad (5.23)$$

$$H_C > r_C \left(1 + \frac{r_R - H_R}{K_C[(r_R - H_R)e_C h_C - e_{RC}]}\right) \quad \text{if } H_R > r_R - \frac{e_{RC}}{e_C h_C} \qquad (5.24)$$

If $H_R < r_R - \frac{e_{RC}}{e_C h_C}$ then we have $H_R < r_R$. If we have $H_R > r_R$ in (5.24), then

we have that $H_C > r_C$. This contradicts the condition needed for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C\right)$ to be biologically relevant; namely that $H_C < r_C$. So, in order to have either of inequalities (5.23) or (5.24), we must have $H_R < r_R$. Additionally, it is necessary to have $e_{RC} < r_R e_C h_C$ in order to have $H_R > 0$ in inequality (5.23). But when this is the case, the condition that $H_C < r_C$ implies inequality (5.23). $\qquad\square$

Biological Remarks: This situation presents some interesting results, which we will discuss in section 7.9.

5.4 Harvesting the Resource in the Full Model

If we harvest only the resource, the form of the full model is

$$
\begin{aligned}
\frac{dR}{dt} &= (r_R - H_R)R\left(1 - \frac{R}{\left(\frac{r_R - H_R}{r_R}\right)K_R}\right) - \frac{e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C + e_{CP}h_{PC}P} \\
&\quad - \frac{e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} \\
\frac{dC}{dt} &= r_C C\left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC}e_{RC}RC}{1 + e_{RC}h_{RC}R + e_C h_C C + e_{CP}h_{PC}P} \\
&\quad - \frac{e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} \\
\frac{dP}{dt} &= \frac{\alpha_{RP}e_{RP}RP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} + \frac{\alpha_{CP}e_{CP}CP}{1 + e_{RP}h_{RP}R + e_{CP}h_{CP}C + e_P h_P P} \\
&\quad - m_P P
\end{aligned}
\tag{5.25}
$$

5.4.1 Invasion and Exclusion When All Species are Absent

The eigenvalues of the Jacobian matrix at the equilibrium $(0,0,0)$ are

$$\lambda_1 = r_R - H_R$$

$$\lambda_2 = r_C > 0$$

$$\lambda_3 = -m_P < 0$$

In this case, the consumers will be able to invade the system at $(0,0,0)$ and the predators will be excluded at $(0,0,0)$. If $H_R < r_R$ then $\lambda_1 > 0$ and the resource will be able to invade the system at $(0,0,0)$. If $H_R > r_R$ then $\lambda_1 < 0$ and the resource will be excluded from the system. In either case, $(0,0,0)$ is a saddle.

5.4.2 Invasion and Exclusion When the Consumers and Predators are Absent

If $H_R < r_R$, then the equilibrium $\left(\left(\frac{r_R - H_R}{r_R} \right) K_R, 0, 0 \right)$ is biologically relevant. In this case, the eigenvalues of the Jacobian matrix are

$$\lambda_1 = H_R - r_R < 0$$

$$\lambda_2 = r_C + \frac{\alpha_{RC} e_{RC} \left(\frac{r_R - H_R}{r_R} \right) K_R}{1 + e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R} \right) K_R}$$

$$\lambda_3 = -m_P + \frac{\alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R} \right) K_R}{1 + e_{RP} h_{RP} \left(\frac{r_R - H_R}{r_R} \right) K_R}$$

If $\lambda_2 > 0$ then the consumers will be able to invade the system at

$\left(\left(\frac{r_R-H_R}{r_R}\right)K_R, 0, 0\right)$. But,

$$\lambda_2 > 0 \Leftrightarrow r_C > \frac{\alpha_{RC}e_{RC}(H_R - r_R)K_R}{r_R + e_{RC}h_{RC}(H_R - r_R)K_R} \tag{5.26}$$

$$\Leftrightarrow \begin{cases} H_R < r_R\left(1 + \frac{r_C}{e_{RC}K_R(\alpha_{RC} - r_C h_{RC})}\right) & \text{if } r_C > \frac{\alpha_{RC}}{h_{RC}} \\ H_R > r_R\left(1 + \frac{r_C}{e_{RC}K_R(\alpha_{RC} - r_C h_{RC})}\right) & \text{if } r_C < \frac{\alpha_{RC}}{h_{RC}} \end{cases} \tag{5.27}$$

Notice that in the case where $r_C < \frac{\alpha_{RC}}{h_{RC}}$, we get that $H_R > r_R$, since $r_R\left(1 + \frac{r_C}{e_{RC}K_R(\alpha_{RC} - r_C h_{RC})}\right) > r_R$. This contradicts the condition needed to have $\left(\left(\frac{r_R-H_R}{r_R}\right)K_R, 0, 0\right)$ be biologically relevant; namely that $H_R < r_R$. Thus, in order for the consumers to be able to invade the system at $\left(\left(\frac{r_R-H_R}{r_R}\right)K_R, 0, 0\right)$, we either need to have $H_R < r_R$ with $r_C > \frac{\alpha_{RC}e_{RC}(H_R-r_R)K_R}{r_R + e_{RC}h_{RC}(H_R-r_R)K_R}$ or $r_C > \frac{\alpha_{RC}}{h_{RC}}$ with $H_R < r_R\left(1 + \frac{r_C}{e_{RC}K_R(\alpha_{RC} - r_C h_{RC})}\right)$.

Biological Remark: When we have $H_R < r_R$ with $r_C > \frac{\alpha_{RC}e_{RC}(H_R-r_R)K_R}{r_R + e_{RC}h_{RC}(H_R-r_R)K_R}$, there can be more harvesting of the resource yet the consumers don't need as large an intrinsic growth rate in order to be able to invade. But when we have $r_C > \frac{\alpha_{RC}}{h_{RC}}$ with $H_R < r_R\left(1 + \frac{r_C}{e_{RC}K_R(\alpha_{RC} - r_C h_{RC})}\right)$, then there is less harvesting yet the consumers need have a higher intrinsic growth rate in order to be able to invade. This seems counterintuitive. It would seem that less harvesting would mean more food for the consumers, and more food for the consumers seems like it would mean that the consumers do not need to have as large of an intrinsic growth rate to still be able to invade. But when $r_C > \frac{\alpha_{RC}}{h_{RC}}$, the consumers are sufficiently inefficient at gaining for consuming the resource. So, harvesting the resource more helps keep the consumers from wasting time feeding upon the resource, which they gain sufficiently little from. This benefit means the consumers do not need as large of an intrinsic growth rate in order to invade.

The predators will be able to invade the system at $\left(\left(\frac{r_R-H_R}{r_R}\right)K_R, 0, 0\right)$ if $\lambda_3 > 0$.

But,

$$\lambda_3 > 0 \Leftrightarrow m_P < \frac{\alpha_{RP}}{h_{RP}} \left(\frac{e_{RP}(r_R - H_R)K_R}{\frac{r_R}{h_{RP}} + e_{RP}(r_R - H_R)K_R} \right) \tag{5.28}$$

$$\Leftrightarrow \begin{cases} H_R > r_R \left(1 + \frac{m_P}{e_{RP}K_R(m_P h_{RP} - \alpha_{RP})} \right) & \text{if } m_P > \frac{\alpha_{RP}}{h_{RP}} \\ H_R < r_R \left(1 + \frac{m_P}{e_{RP}K_R(m_P h_{RP} - \alpha_{RP})} \right) & \text{if } m_P < \frac{\alpha_{RP}}{h_{RP}} \end{cases} \tag{5.29}$$

Notice that if $m_P > \frac{\alpha_{RP}}{h_{RP}}$, then we cannot have $H_R > r_R \left(1 + \frac{m_P}{e_{RP}K_R(m_P h_{RP} - \alpha_{RP})} \right)$ because this would imply that $H_R > r_R$, which contradicts the condition needed in order to have $\left(\left(\frac{r_R - H_R}{r_R} \right) K_R, 0, 0 \right)$ be biologically relevant; namely that $H_R < r_R$. Thus, in order for the predators to be able to invade the system at $\left(\left(\frac{r_R - H_R}{r_R} \right) K_R, 0, 0 \right)$, we either need to have $H_R < r_R$ with $m_P < \frac{\alpha_{RP}e_{RP}(r_R - H_R)K_R}{r_R + e_{RP}h_{RP}(r_R - H_R)K_R}$ or $m_P < \frac{\alpha_{RP}}{h_{RP}}$ with $H_R < r_R \left(1 + \frac{m_P}{e_{RP}K_R(m_P h_{RP} - \alpha_{RP})} \right)$.

Biological Remark: When $m_P < \frac{\alpha_{RP}}{h_{RP}}$, there can be a higher natural mortality rate for the predators than when $m_P < \frac{\alpha_{RP}}{h_{RP}} \left(\frac{e_{RP}(r_R - H_R)K_R}{\frac{r_R}{h_{RP}} + e_{RP}(r_R - H_R)K_R} \right)$. But when $m_P < \frac{\alpha_{RP}}{h_{RP}}$, there cannot be as much harvesting of the resource as the case where $m_P < \frac{\alpha_{RP}}{h_{RP}} \left(\frac{e_{RP}(r_R - H_R)K_R}{\frac{r_R}{h_{RP}} + e_{RP}(r_R - H_R)K_R} \right)$. This makes sense as the resource is the only food source for the predators. The higher the predators' natural mortality rate, the less the resource can be harvested in order for the predators to avoid being excluded from the system because of a lack of food. Likewise, the lower the predators' natural mortality rate, the less food it needs in order to be able to invade. This means more harvesting of the resource that can be done while not excluding the predators from the system.

5.4.3 Invasion and Exclusion When the Resource and Predators are Absent

The eigenvalues of the Jacobian matrix at $(0, K_C, 0)$ are

$$\lambda_1 = (r_R - H_R)\left(1 - \frac{e_{RC}K_C}{1 + e_C h_C K_C}\right)$$

$$\lambda_2 = -r_C < 0$$

$$\lambda_3 = -m_P + \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

The resource will be able to invade the system at $(0, K_C, 0)$ when $\lambda_1 > 0 \Leftrightarrow H_R < r_R$ and $e_{RC}K_C < 1 + e_C h_C K_C$.

The predators will be able to invade the system at $(0, K_C, 0)$ when $\lambda_3 > 0 \Leftrightarrow$ $m_P < \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$.

5.4.4 Invasion and Exclusion When the Consumers are Absent

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_R e_{RP}h_{RP}\right) > 0$, invasibility condition (4.46) becomes

$$r_C > \frac{2e_{CP}\alpha_{RP}}{e_P h_P(\alpha_{RP} - m_P h_{RP})} - \frac{\frac{1}{2}\alpha_{RC}e_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R}{1 + \left(e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_P h_P m_P}\right)\left(\frac{r_R - H_R}{r_R}\right)K_R} \quad (5.30)$$

and exclusion condition (4.47) becomes

$$
\begin{aligned}
r_C < & \frac{e_{CP}\left[\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R - m_P\left(1+\left(\frac{r_R-H_R}{r_R}\right)K_R e_{RP}h_{RP}\right)\right]}{e_P h_P m_P}}{1+\left(e_{RP}h_{RP}+\frac{\alpha_{RP}e_{RP}}{m_P}\right)\left(\frac{r_R-H_R}{r_R}\right)K_R} \\
& - \frac{\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1+\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{CP}\left[\frac{\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R - m_P\left(1+\left(\frac{r_R-H_R}{r_R}\right)K_R e_{RP}h_{RP}\right)}{e_P h_P m_P}\right]}
\end{aligned}
$$

$$(5.31)$$

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R - m_P\left(1+\left(\frac{r_R-H_R}{r_R}\right)K_R e_{RP}h_{RP}\right) < 0$, invasibility condition (4.48) becomes

$$
r_C > \frac{\frac{e_{CP}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{e_P h_P m_P}}{1+\frac{1}{2}e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R} - \frac{\frac{1}{2}\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1+e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{e_P h_P m_P}}
$$

$$(5.32)$$

and exclusion condition (4.49) becomes

$$
r_C < -\frac{\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1+\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}.
$$

$$(5.33)$$

Before stating the following theorem, we introduce some terminology.

Definition 5.1.   *1. We say that increasing H_R makes it easier for the consumers to invade if the right hand side of either invasibility condition (5.30) or (5.32) is a decreasing function of H_R; i.e., if increasing H_R reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing H_R makes it harder for the consumers to invade if the right hand side of either invasibility condition (5.30) or (5.32) is an increasing function of H_R; i.e., if increasing H_R increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing H_R makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (5.31) or (5.33) is an increasing

function of H_R; i.e., if increasing H_R increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing H_R makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (5.31) or (5.33) is a decreasing function of H_R; i.e., if increasing H_R decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 5.10. *Increasing H_R*

1. *makes invasion easier if*

   (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) < 0,\ m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}},$ *and*
      $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}.$

   (b) $m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ *and* $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}.$

2. *makes invasion harder if*

   (a) $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) > 0$ *and* $m_P <$
      $\frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}.$

   (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) < 0,\ m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}},$ *and*
      $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}.$

   (c) $m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ *and* $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}.$

3. *makes exclusion easier if*

   (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) > 0,\ m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}},\ e_{CP}h_{CP} <$
      $e_Ph_P,$ *and* $e_{CP} << e_{RC}.$

   (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) < 0$ *and* $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}.$

4. *makes exclusion harder if*

   (a) $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) > 0,\ m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}},$
      and $e_{CP}h_{CP} > e_Ph_P.$

(b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_R e_{RP}h_{RP}\right) > 0$, $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$, $e_{CP}h_{CP} < e_P h_P$, and $e_{CP} >> e_{RC}$.

Proof. Having the condition $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + \left(\frac{r_R - H_R}{r_R}\right)K_R e_{RP}h_{RP}\right) > 0$ is equivalent to

$$
H_R \begin{cases} > r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right)}\right] & \text{if } m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}} \\[2ex] < r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP} - m_P h_{RP}\right)}\right] & \text{if } m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}} \end{cases}
$$

Since we must have $H_R < r_R$ in order for R^* to be biologically relevant, we cannot have the case where $m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ because this would imply that $H_R > r_R$.

The first fraction on the right hand side of invasibility condition (5.30) is independent of H_R. The second fraction on the right hand side of invasibility condition (5.30) is of the form

$$
g(H_R) = \frac{E - FH_R}{G - IH_R}
$$

where

$$
E = \frac{1}{2}\alpha_{RC}e_{RC}K_R
$$
$$
F = \frac{\alpha_{RC}e_{RC}K_R}{2r_R}
$$
$$
G = 1 + e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_P h_P m_P}
$$
$$
H = \frac{1}{r_R}\left(e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_P h_P m_P}\right)
$$

We have that

$$
g'(H_R) = \frac{EI - FG}{(G - IH_R)^2} \begin{cases} > 0 \text{ if } EI > FG \\[2ex] < 0 \text{ if } EI < FG \end{cases}.
$$

Note that

$$EI > FG \Leftrightarrow \frac{\alpha_{RC}e_{RC}K_R}{2r_R}\left(e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_Ph_Pm_P}\right)$$
$$> \frac{\alpha_{RC}e_{RC}K_R}{2r_R}\left(1 + e_{RC}h_{RC} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}}{e_Ph_Pm_P}\right)$$
$$\Leftrightarrow 0 > 1$$

and

$$EI < FG \Leftrightarrow 0 < 1.$$

Thus, we must have that $g'(H_R) < 0$. So, increasing H_R causes the second fraction right hand side of invasibility condition (5.30) to decrease. But since we are subtracting this fraction, we get that increasing H_R causes the right hand side of invasibility condition (5.30) to increase. This makes invasion harder.

The first fraction on the right hand side of exclusion condition (5.31) is of the form
$$f(H_R) = \frac{A + BH_R}{C - DH_R}$$

where

$$A = e_{CP}\left[\frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)}{e_Ph_Pm_P}\right]$$
$$B = e_{CP}\left(\frac{-\frac{\alpha_{RP}e_{RP}K_R}{2r_R} + \frac{m_Pe_{RP}h_{RP}K_R}{r_R}}{e_Ph_Pm_P}\right)$$
$$C = 1 + e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}$$
$$D = \frac{e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}}{r_R}$$

Here, B could be positive or negative. We have that

$$f'(H_R) = \frac{BC + AD}{(C - DH_R)^2} \begin{cases} > 0 \text{ if } B > -\frac{AD}{C} \\ \\ < 0 \text{ if } B < -\frac{AD}{C} \end{cases}.$$

Note that

$$B > -\frac{AD}{C} \Leftrightarrow -\frac{e_{CP}}{r_R e_P h_P m_P}\left(\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P e_{RP}h_{RP}K_R\right)$$

$$> -\frac{\frac{e_{CP}}{r_R e_P h_P m_P}\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)\right]\left(e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}\right)}{1 + e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}}$$

$$\Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P e_{RP}h_{RP}K_R$$

$$< \frac{\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)\right]\left(e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}\right)}{1 + e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}}$$

But

$$\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R) < \frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P e_{RP}h_{RP}K_R$$

and

$$\frac{e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}}{1 + e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}} < 1$$

so

$$\frac{\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)\right]\left(e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}\right)}{1 + e_{RP}h_{RP}K_R + \frac{\alpha_{RP}e_{RP}K_R}{m_P}}$$

$$< \frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P e_{RP}h_{RP}K_R$$

Therefore, we have $B < -\frac{AD}{C}$ which tells us that we must have $f'(H_R) < 0$. Thus, increasing H_R causes the first fraction on the right hand side of exclusion condition (5.31) to decrease.

The second fraction on the right hand side of exclusion condition (5.31) is of the

form

$$g(H_R) = \frac{A - BH_R}{C + DH_R}$$

where

$$A = \alpha_{RC} e_{RC} K_R$$

$$B = \frac{\alpha_{RC} e_{RC} K_R}{r_R}$$

$$C = 1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_{CP} h_{CP} \left[\frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + e_{RP} h_{RP} K_R)}{e_P h_P m_P} \right]$$

$$D = -\frac{e_{RC} h_{RC} K_R}{2r_R} + e_{CP} h_{CP} \left(\frac{-\frac{\alpha_{RP} e_{RP} K_R}{2r_R} + \frac{e_{RP} h_{RP} K_R m_P}{r_R}}{e_P h_P m_P} \right)$$

Here, C and D could be positive or negative. We have that

$$g'(H_R) = -\frac{BC + AD}{(C + DH_R)^2} \begin{cases} > 0 \text{ if } BC < -AD \\ \\ < 0 \text{ if } BC > -AD \end{cases}.$$

Note that

$$BC < -AD \Leftrightarrow \frac{\alpha_{RC} e_{RC} K_R}{r_R} \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R + e_{CP} h_{CP} \left[\frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + e_{RP} h_{RP} K_R)}{e_P h_P m_P} \right] \right)$$

$$< -\alpha_{RC} e_{RC} K_R \left[-\frac{e_{RC} h_{RC} K_R}{2r_R} + e_{CP} h_{CP} \left(\frac{-\frac{\alpha_{RP} e_{RP} K_R}{2r_R} + \frac{e_{RP} h_{RP} K_R m_P}{r_R}}{e_P h_P m_P} \right) \right]$$

$$\Leftrightarrow \frac{1}{r_R} + \frac{e_{RC} h_{RC} K_R}{2r_R} + \frac{e_{CP} h_{CP}}{r_R} \left[\frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + e_{RP} h_{RP} K_R)}{e_P h_P m_P} \right] - \frac{e_{CP} h_{CP}}{r_R e_P h_P}$$

$$< \frac{e_{RC} h_{RC} K_R}{2r_R} + \frac{e_{CP} h_{CP}}{r_R} \left(\frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P e_{RP} h_{RP} K_R}{e_P h_P m_P} \right)$$

$$\Leftrightarrow \frac{1}{r_R} - \frac{e_{CP} h_{CP}}{r_R e_P h_P} < 0$$

$$\Leftrightarrow e_{CP} h_{CP} > e_P h_P$$

and

$$BC > -AD \Leftrightarrow e_{CP} h_{CP} < e_P h_P.$$

So, if $e_{CP} h_{CP} > e_P h_P$, then increasing H_R causes the second fraction on the right hand

side of exclusion condition (5.31) to increase. But if $e_{CP}h_{CP} < e_Ph_P$, then increasing H_R causes the second fraction on the right hand side of exclusion condition (5.31) to decrease.

So, if $e_{CP}h_{CP} > e_Ph_P$, then when we subtract the second fraction from the first fraction on the right hand side of exclusion condition (5.31), we get that the right hand side is decreasing as a result of increasing H_R. In this case, exclusion is harder. If $e_{CP}h_{CP} < e_Ph_P$, then when we subtract the second fraction from the first fraction on the right hand side of exclusion condition (5.31), we get that the right hand side could be increasing or decreasing as a result of increasing H_R. If $e_{CP} >> e_{RC}$, then the first fraction on the right hand side of exclusion condition (5.31) will dominate the second fraction. In this case, this means the right hand side of exclusion condition (5.31) will be decreasing as a result of increasing H_R. This makes exclusion harder. But in the case where $e_{CP} << e_{RC}$, then the second fraction on the right hand side of exclusion condition (5.31) will dominate the first fraction. In this case, this means the right hand side of exclusion condition (5.31) will be increasing as a result of increasing H_R. This makes exclusion easier.

The condition $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R - m_P\left(1 + \left(\frac{r_R-H_R}{r_R}\right)K_Re_{RP}h_{RP}\right) < 0$ is equivalent to

$$H_R \begin{cases} < r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right] & \text{if } m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}} \\ > r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right] & \text{if } m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}. \end{cases}$$

Since we must have $H_R < r_R$ in order for R^* to be biologically relevant, if $m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$, then we will always be in this case.

The first fraction on the right hand side of invasibility condition (5.32) is of the form

$$f(H_R) = \frac{A - BH_R}{C - DH_R}$$

where

$$A = \frac{e_{CP}\alpha_{RP}e_{RP}K_R}{e_P h_P m_P}$$

$$B = \frac{e_{CP}\alpha_{RP}e_{RP}K_R}{e_P h_P m_P r_R}$$

$$C = 1 + \frac{1}{2}e_{RP}h_{RP}K_R$$

$$D = \frac{e_{RP}h_{RP}K_R}{2r_R}$$

We have that

$$f'(H_R) = \frac{AD - BC}{(C - DH_R)^2} \begin{cases} > 0 \text{ if } AD > BC \\ \\ < 0 \text{ if } AD < BC \end{cases}.$$

Note that

$$AD > BC \Leftrightarrow \frac{e_{CP}\alpha_{RP}e_{RP}K_R^2 e_{RP}h_{RP}}{2e_P h_P m_P r_R} > \frac{e_{CP}\alpha_{RP}e_{RP}K_R\left(1 + \frac{1}{2}e_{RP}h_{RP}K_R\right)}{e_P h_P m_P r_R}$$

$$\Leftrightarrow \frac{1}{2}K_R e_{RP}h_{RP} > 1 + \frac{1}{2}e_{RP}h_{RP}K_R$$

$$\Leftrightarrow 0 > 1$$

and

$$AD < BC \Leftrightarrow 0 < 1.$$

Thus, we must have $f'(H_R) < 0$.

The second fraction on the right hand side of invasibility condition (5.32) is of the form

$$g(H_R) = \frac{E - FH_R}{G - IH_R}$$

where

$$E = \frac{1}{2}\alpha_{RC}e_{RC}K_R$$

$$F = \frac{\alpha_{RC}e_{RC}K_R}{2r_R}$$

$$G = 1 + e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}K_R}{e_P h_P m_P}$$

$$H = \frac{e_{RC}h_{RC}K_R}{r_R} + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}K_R}{r_R e_P h_P m_P}$$

We have that $g'(H_R) > 0$ if $EI > FG$ and $g'(H_R) < 0$ if $EI < FG$. Note that

$$EI > FG \Leftrightarrow \frac{\alpha_{RC}e_{RC}K_R}{2r_R}\left(e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}K_R}{e_P h_P m_P}\right)$$

$$> \frac{\alpha_{RC}e_{RC}K_R}{2r_R}\left(1 + e_{RC}h_{RC}K_R + \frac{e_{CP}h_{CP}\alpha_{RP}e_{RP}K_R}{e_P h_P m_P}\right)$$

$$\Leftrightarrow 0 > 1$$

and

$$EI < FG \Leftrightarrow 0 < 1.$$

Thus, we must have $g'(H_R) < 0$.

So, increasing H_R causes both the first and second fraction on the right hand side of invasibility condition (5.32) to decrease. But when we subtract the second fraction from the first fraction, we get that the right hand side could be increasing or decreasing. If $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$ then the first fraction on the right hand side of invasibility condition (5.32) dominates the second fraction. In this case, increasing H_R causes the right hand side of the invasibility condition to decrease, which makes invasion easier. But if $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$ then the second fraction on the right hand side of invasibility condition (5.32) dominates the first fraction. In this case, increasing H_R causes the right hand side of the invasibility to increase, which makes invasion harder.

The right hand side of exclusion condition (5.33) is of the form

$$f(H_R) = \frac{-A + BH_R}{C - DH_R}$$

where

$$A = \alpha_{RC} e_{RC} K_R$$

$$B = \frac{\alpha_{RC} e_{RC} K_R}{r_R}$$

$$C = 1 + \frac{1}{2} e_{RC} h_{RC} K_R$$

$$D = \frac{e_{RC} h_{RC} K_R}{2 r_R}$$

We have that

$$f'(H_R) = \frac{BC - AD}{(C - DH_R)^2} \begin{cases} > 0 \text{ if } BC > DA \\ \\ < 0 \text{ if } BC < DA \end{cases}.$$

Note that

$$BC > DA \Leftrightarrow \frac{\alpha_{RC} e_{RC} K_R \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)}{r_R} > \frac{\alpha_{RC} e_{RC} K_R e_{RC} h_{RC} K_R}{2 r_R}$$

$$\Leftrightarrow 1 + \frac{1}{2} e_{RC} h_{RC} K_R > \frac{1}{2} e_{RC} h_{RC} K_R$$

$$\Leftrightarrow 1 > 0$$

and

$$BC < DA \Leftrightarrow 1 < 0.$$

So we must have $f'(H_R) > 0$. Thus, increasing H_R causes the right hand side of exclusion condition (5.33) to increase, which makes exclusion easier. $\square$

5.4.5 Invasion and Exclusion when Predators are Absent

In the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R < 1 + e_C h_C K_C$, invasibility condition (4.54) becomes

$$m_P < \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{RP} h_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R + e_{CP} h_{CP} K_C \left(1 + \frac{\alpha_{RC} e_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}{r_C (1 + e_C h_C K_C)}\right)} \tag{5.34}$$

and exclusion condition (4.55) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{CP} h_{PC} K_C} + \frac{\alpha_{CP} e_{CP} K_C \left(1 + \frac{\alpha_{RC} e_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}{r_C (1 + e_C h_C K_C)}\right)}{1 + e_{CP} h_{CP} K_C}. \tag{5.35}$$

In the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $1 + e_C h_C K_C < e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R$, invasibility condition (4.56) becomes

$$m_P < \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{RP} h_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R + e_{CP} h_{CP} K_C \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)} \tag{5.36}$$

and exclusion condition (4.57) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{CP} h_{PC} K_C} + \frac{\alpha_{CP} e_{CP} K_C \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}{1 + e_{CP} h_{CP} K_C}. \tag{5.37}$$

Before stating the following theorem, we introduce some terminology.

Definition 5.2. *1. We say that increasing H_R makes it easier for the predators to invade if the right hand side of either invasibility condition (5.34) or (5.36) is an increasing function of H_R; i.e., if increasing H_R increases the maximum value of m_P, allowed for the predators to invade. We say that increasing H_R makes it harder for the predators to invade if the right hand side of either invasibility condition (5.34) or (5.36) is a decreasing function of H_R; i.e., if increasing H_R*

reduces the maximum value of m_P allowed for the predators to invade.

2. *We say that increasing H_R makes it easier for the predators to be excluded if the right hand side of either exclusion condition (5.35) or (5.37) is a decreasing function of H_R; i.e., if increasing H_R decreases the minimum value of m_P which results in the predators being excluded. We say that increasing H_R makes it harder for the predators to be excluded if the right hand side of either exclusion condition (5.35) or (5.37) is an increasing function of H_R; i.e., if increasing H_R increases the minimum value of m_P which results in the predators being excluded.*

Theorem 5.11. *Increasing H_R*

1. *makes invasion easier.*

2. *makes exclusion easier.*

Proof. We are first in the case where $e_{RC}h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R < 1 + e_C h_C K_C \Leftrightarrow H_R > r_R\left(1 - \frac{1 + e_C h_C K_C}{e_{RC}h_{RC}K_R}\right)$. Note that it is necessary to have $H_R < r_R$ in order to have $R^* > 0$, and the second condition will be trivially satisfied if $1 + e_C h_C K_C > e_{RC}h_{RC}K_R$.

The right hand side of invasibility condition (5.34) is of the form

$$f(H_R) = \frac{A}{B - CH_R}$$

where

$$A = \alpha_{CP}e_{CP}K_C$$

$$B = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C(1 + e_C h_C K_C)}\right)$$

$$C = \frac{e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R}{1 + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R}{r_C(1 + e_C h_C K_C)}\right)}{1 + e_{CP}h_{CP}K_C}$$

We have that $f'(H_R) > 0$. Thus, increasing H_R causes the right hand side of invasibility condition (5.34) to increase, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (5.35) is of the form

$$f(H_R) = A - BH_R$$

where

$$A = \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{CP} h_{PC} K_C}$$

$$B = \frac{\alpha_{RP} e_{RP} K_R}{r_R (1 + e_{CP} h_{PC} K_C)}$$

We have that $f'(H_R) < 0$, so increasing H_R causes the first fraction on the right hand side of exclusion condition (5.35) to decrease.

The second fraction on the right hand side of exclusion condition (5.35) is of the form

$$g(H_R) = C - DH_R$$

where

$$C = \frac{\alpha_{CP} e_{CP} K_C \left(1 + \frac{\alpha_{RC} e_{RC} K_R}{r_C (1 + e_C h_C K_C)}\right)}{1 + e_{CP} h_{CP} K_C}$$

$$D = \frac{\frac{\alpha_{CP} e_{CP} K_C \alpha_{RC} e_{RC} K_R}{r_R r_C (1 + e_C h_C K_C)}}{1 + e_{CP} h_{CP} K_C}$$

We have that $g'(H_R) < 0$, so increasing H_R causes the second fraction on the right hand side of exclusion condition (5.35) to decrease.

Thus, increasing H_R causes both the first and second fractions on the right hand side of exclusion condition (5.35) to decrease. When we add these two fractions together, we get that the right hand side of exclusion condition (5.35) is decreasing. This makes exclusion easier.

We are next in the case where $1 + e_C h_C K_C < e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R} \right) K_R \Leftrightarrow H_R < r_R \left(1 - \frac{1 + e_C h_C K_C}{e_{RC} h_{RC} K_R} \right)$. Note that we must have $e_{RC} h_{RC} K_R > 1 + e_C h_C K_C$ because otherwise, we will have $H_R < 0$. Provided we have $e_{RC} h_{RC} K_R > 1 + e_C h_C K_C$, then $H_R < r_R \left(1 - \frac{1 + e_C h_C K_C}{e_{RC} h_{RC} K_R} \right) \Rightarrow H_R < r_R$, so we will have $R^* > 0$.

The right hand side of invasibility condition (5.36) is of the form

$$f(H_R) = \frac{A}{B - C H_R}$$

where

$$A = \alpha_{CP} e_{CP} K_C$$

$$B = 1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} K_C \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}} \right)$$

$$C = \frac{e_{RP} h_{RP} K_R}{r_R}$$

We have that $f'(H_R) > 0$. Thus, increasing H_R causes the right hand side of invasibility condition (5.36) to increase, which makes invasion easier.

The second fraction on the right hand side of exclusion condition (5.37) is independent of H_R. The first fraction on the right hand side of exclusion condition (5.37) is of the form

$$f(H_R) = A - B H_R$$

where

$$A = \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{CP} h_{PC} K_C}$$

$$B = \frac{\alpha_{RP} e_{RP} K_R}{r_R (1 + e_{CP} h_{PC} K_C)}$$

We have that $f'(H_R) < 0$. Thus, increasing H_R causes the right hand side of exclusion condition (5.37) to decrease, which makes exclusion easier. So in both cases, the

conclusions are the same. □

In the case where $\frac{1}{2}\left(\frac{r_R-H_R}{r_R}\right)K_R < R^* < \left(\frac{r_R-H_R}{r_R}\right)K_R$ and $\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R$ $< 1 + e_C h_C K_C$, invasibility condition (4.68) becomes

$$m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1 + e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_C h_C K_C\right)}\right)}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_C h_C K_C\right)}\right)}$$

(5.38)

and exclusion condition (4.69) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1 + \frac{1}{2}e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{PC}K_C}$$
$$+ \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}e_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R}{r_C\left(1+\frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_C h_C K_C\right)}\right)}{1 + \frac{1}{2}e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{CP}K_C}$$

(5.39)

Note that it is necessary to have $H_R < r_R$ in order to have $R^* > 0$, and the second condition will be trivially satisfied if $1 + e_C h_C K_C > \frac{1}{2}e_{RC}h_{RC}K_R$. In this case, the calculations and expressions become prohibitively long and complicated, and drawing useful conclusions becomes difficult. However, we can obtain useful information is some special cases. For instance, in the case where $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$, the first fraction in exclusion condition (5.39) dominates the second fraction, so effectively, the exclusion condition becomes

$$m_P > \frac{\alpha_{RP}e_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R}{1 + \frac{1}{2}e_{RP}h_{RP}\left(\frac{r_R-H_R}{r_R}\right)K_R + e_{CP}h_{PC}K_C}.$$

(5.40)

Before stating the following theorem, we introduce some terminology.

Definition 5.3. *We say that increasing H_R makes it easier for the predators to be excluded if the right hand side of exclusion condition (5.40) is a decreasing function of H_R; i.e., if increasing H_R decreases the minimum value of m_P which results in the predators being excluded.*

Theorem 5.12. *Increasing H_R makes exclusion easier.*

Proof. The right hand side of exclusion condition (5.40) is of the form

$$f(H_R) = \frac{A - BH_R}{C - DH_R}$$

where

$$A = \alpha_{RP}e_{RP}K_R$$
$$B = \frac{\alpha_{RP}e_{RP}K_R}{r_R}$$
$$C = 1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C$$
$$D = \frac{e_{RP}h_{RP}K_R}{2r_R}$$

We have that

$$f'(H_R) = \frac{AD - BC}{(C - DH_R)^2} \begin{cases} > 0 \text{ if } AD > BC \\ \\ < 0 \text{ if } AD < BC \end{cases}$$

Note that

$$AD > BC \Leftrightarrow \frac{e_{RP}h_{RP}K_R^2\alpha_{RP}e_{RP}}{2r_R} > \frac{\alpha_{RP}e_{RP}K_R \left(1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\right)}{r_R}$$
$$\Leftrightarrow \frac{1}{2}e_{RP}h_{RP}K_R > 1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C$$
$$\Leftrightarrow 0 > 1 + e_{CP}h_{PC}K_C$$

and

$$AD < BC \Leftrightarrow 0 < 1 + e_{CP}h_{PC}K_C.$$

So, we must have $f'(H_R) < 0$. Thus, when $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$, increasing H_R causes the right hand side of exclusion condition (5.40) to decrease, which makes exclusion easier. $\square$

In the case where $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right)K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right)K_R$ and $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R$, invasibility condition (4.72) becomes

$$
\begin{aligned}
m_P < \ & \frac{\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R}{1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)} \\
& + \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R + e_{CP}h_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}
\end{aligned}
\tag{5.41}
$$

and exclusion condition (4.73) becomes

$$
m_P > \frac{\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R}{1 + \frac{1}{2}e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R + e_{CP}h_{PC}K_C} + \frac{\alpha_{CP}e_{CP}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)}{1 + e_{CP}h_{CP}K_C}.
\tag{5.42}
$$

Note that we require $H_R < r_R$ in order to guarantee that $R^* > 0$.

Before stating the following theorem, we introduce some terminology.

Definition 5.4. *1. We say that increasing H_R makes it easier for the predators to invade if the right hand side of either invasibility condition (5.41) is an increasing function of H_R; i.e., if increasing H_R increases the maximum value of m_P, allowed for the predators to invade. We say that increasing H_R makes it harder for the predators to invade if the right hand side of either invasibility condition (5.41) is a decreasing function of H_R; i.e., if increasing H_R reduces the maximum value of m_P allowed for the predators to invade.*

2. We say that increasing H_R makes it easier for the predators to be excluded if the right hand side of either exclusion condition (5.42) is a decreasing function of H_R; i.e., if increasing H_R decreases the minimum value of m_P which results in

the predators being excluded. We say that increasing H_R makes it harder for the predators to be excluded if the right hand side of either exclusion condition (5.42) is an increasing function of H_R; i.e., if increasing H_R increases the minimum value of m_P which results in the predators being excluded.

Theorem 5.13. *Increasing H_R*

1. *makes invasion easier if $\alpha_{RP}e_{RP}K_R << \alpha_{CP}e_{CP}K_C$.*

2. *makes invasion harder if $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$.*

3. *makes exclusion easier.*

Proof. The first fraction on the right hand side of invasibility condition (5.41) is of the form

$$f(H_R) = \frac{A - BH_R}{C - DH_R}$$

where

$$A = \frac{1}{2}\alpha_{RP}e_{RP}K_R$$

$$B = \frac{\alpha_{RP}e_{RP}K_R}{2r_R}$$

$$C = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

$$D = \frac{e_{RP}h_{RP}K_R}{r_R}$$

We have that $f'(H_R) > 0$ if $AD > BC$ and $f'(H_R) < 0$ if $AD < BC$. Note that

$$AD > BC \Leftrightarrow \frac{\alpha_{RP}e_{RP}^2 K_R^2 h_{RP}}{2r_R} > \frac{\alpha_{RP}e_{RP}K_R\left[1 + e_{RP}h_{RP}K_R e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)\right]}{2r_R}$$

$$\Leftrightarrow e_{RP}h_{RP}K_R > 1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

$$\Leftrightarrow 0 > 1 + e_{CP}h_{PC}K_C\left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

and

$$AD < BC \Leftrightarrow 0 < 1 + e_{CP}h_{PC}K_C \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right).$$

So, we must have $f'(H_R) < 0$. So, increasing H_R causes the first fraction on the right hand side of invasibility condition (5.41) to decrease.

The second fraction on the right hand side of invasibility condition (5.41) is of the form

$$g(H_R) = \frac{A}{B - CH_R}$$

where

$$A = \alpha_{CP}e_{CP}K_C$$

$$B = 1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C \left(1 + \frac{\alpha_{RC}}{r_C h_{RC}}\right)$$

$$C = \frac{e_{RP}h_{RP}K_R}{r_R}$$

We have that $g'(H_R) > 0$, so increasing H_R causes the second fraction on the right hand side of invasibility condition (5.41) to increase.

Thus, increasing H_R causes the first fraction on the right hand side of invasibility condition (5.41) to decrease, while causing the second fraction to increase. When we add these fractions together, the result could be increasing or decreasing. If $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$ then the first fraction on the right hand side of invasibility condition (5.41) will dominate the second fraction. In this case, increasing H_R causes the right hand side of invasibility condition (5.41) to decrease, which makes invasion harder. But if $\alpha_{RP}e_{RP}K_R << \alpha_{CP}e_{CP}K_C$ then the second fraction on the right hand side of invasibility condition (5.41) dominates the first fraction. In this case, increasing H_R causes the right hand side of invasibility condition (5.41) to increase, which makes invasion easier.

The second fraction on the right hand side of exclusion condition (5.42) is inde-

pendent of H_R. The first fraction on the right hand side of exclusion condition (5.42) is of the form

$$f(H_R) = \frac{A - BH_R}{C - DH_R}$$

where

$$A = \alpha_{RP} e_{RP} K_R$$

$$B = \frac{\alpha_{RP} e_{RP} K_R}{r_R}$$

$$C = 1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C$$

$$D = \frac{e_{RP} h_{RP} K_R}{2 r_R}$$

We have that $f'(H_R) > 0$ if $AD > BC$ and $f'(H_R) < 0$ if $AD < BC$. Note that

$$AD > BC \Leftrightarrow \frac{\alpha_{RP} e_{RP}^2 K_R^2 h_{RP}}{2 r_R} > \frac{\alpha_{RP} e_{RP} K_R \left(1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C\right)}{r_R}$$

$$\Leftrightarrow \frac{1}{2} e_{RP} h_{RP} K_R > 1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{PC} K_C$$

$$\Leftrightarrow 0 > 1 + e_{CP} h_{PC} K_C$$

and

$$AD < BC \Leftrightarrow 0 < 1 + e_{CP} h_{PC} K_C.$$

So, we have that $f'(H_R) < 0$. Thus, increasing H_R causes the right hand side of exclusion condition (5.42) to decrease, which makes exclusion easier. □

5.5 Harvesting the Consumers in the Full Model

If we harvest only the consumers, the form of the full model is

$$
\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P}
$$
$$
- \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P}
$$
$$
\frac{dC}{dt} = (r_C - H_C)C \left(1 - \frac{C}{\left(\frac{r_C - H_C}{r_C}\right) K_C}\right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P}
$$

$$(5.43)$$

$$
- \frac{e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P}
$$
$$
\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} + \frac{\alpha_{CP} e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P}
$$
$$
- m_P P
$$

5.5.1 Invasion and Exclusion When All Species are Absent

The eigenvalues of the Jacobian matrix at the equilibrium $(0, 0, 0)$ are

$$
\lambda_1 = r_R > 0
$$
$$
\lambda_2 = r_C - H_C
$$
$$
\lambda_3 = -m_P < 0
$$

In this case, the resource will be able to invade the system at $(0, 0, 0)$ and the predators will be excluded from the system at $(0, 0, 0)$. If $H_C < r_C$ then $\lambda_2 > 0$ and the consumers will be able to invade the system at $(0, 0, 0)$. If $H_C > r_C$ then $\lambda_2 < 0$ and the consumers will be excluded from the system at $(0, 0, 0)$. In either case, $(0, 0, 0)$ is a saddle.

5.5.2   Invasion and Exclusion When the Consumers and Predators are Absent

The eigenvalues of the Jacobian matrix at $(K_R, 0, 0)$ are

$$\lambda_1 = -r_R < 0$$

$$\lambda_2 = r_C - H_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$$

$$\lambda_3 = -m_P + \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R}$$

If $\lambda_2 > 0$ then the consumers will be able to invade the system at $(K_R, 0, 0)$. But,

$$\lambda_2 > 0 \Leftrightarrow H_C < r_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}.$$

Biological Remark: In the case where there is no harvesting, the consumers can always invade at $(K_R, 0, 0)$. In this case, the consumers could be excluded if they are harvested too heavily. But, the consumers can withstand a harvesting rate of $H_C > r_C$ in this case, while still being able to invade the system, provided the level of harvesting does not exceed the combined benefit to the consumers from their intrinsic growth rate plus what they gain from feeding on the resource.

The predators will be able to invade the system when $\lambda_3 > 0 \Leftrightarrow m_P < \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R}$.

5.5.3 Invasion and Exclusion When the Resource and Predators are Absent

If $H_C < r_C$, then the equilibrium $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ is biologically relevant. In this case, the eigenvalues of the Jacobian matrix are

$$\lambda_1 = r_R - \frac{e_{RC}(r_C - H_C)K_C}{r_C + e_C h_C(r_C - H_C)K_C}$$

$$\lambda_2 = H_C - r_C < 0$$

$$\lambda_3 = -m_P + \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$$

If $\lambda_1 > 0$ then the resource will be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$. But,

$$\lambda_1 > 0 \Leftrightarrow r_R > \frac{e_{RC}(r_C - H_C)K_C}{r_C + e_C h_C(r_C - H_C)K_C}$$

$$\Leftrightarrow \begin{cases} H_C < r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) & \text{if } e_{RC} < r_R e_C h_C \\ H_C > r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) & \text{if } e_{RC} > r_R e_C h_C \end{cases}$$

Notice that if $e_{RC} < r_R e_C h_C$ then $r_C \left(1 + \frac{r_R}{K_C(r_R e_C h_C - e_{RC})}\right) > r_C$. But since we must have $H_C < r_C$ in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ to be biologically relevant, then we will have $\lambda_1 > 0$ when $e_{RC} < r_R e_C h_C$.

Biological Remark: If $e_{RC} < r_R e_C h_C$ then the consumers attack the resource a sufficiently small amount of time, the consumers experience a sufficiently large amount of intraspecific interference, the resource has a sufficiently large intrinsic growth rate, or some combination of these. In this case, the resource will always be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$. But, if $e_{RC} > r_R e_C h_C$, then there is some combination of sufficiently large attack rate on the resource by the consumers,

sufficiently small intrinsic growth rate by the resource, or sufficiently small amount of intraspecific interference by the consumers. In this case, the resource will be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ if there is a sufficiently large amount of harvesting on the consumers. If H_C is too small, then the resource will be excluded from the system.

The predators will be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ if $\lambda_3 > 0$. But,

$$\lambda_3 > 0 \Leftrightarrow m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$$

$$\Leftrightarrow \begin{cases} H_C > r_C \left(1 + \frac{m_P}{e_{CP} K_C (m_P h_{CP} - \alpha_{CP})}\right) & \text{if } m_P > \frac{\alpha_{CP}}{h_{CP}} \\ H_C < r_C \left(1 + \frac{m_P}{e_{CP} K_C (m_P h_{CP} - \alpha_{CP})}\right) & \text{if } m_P < \frac{\alpha_{CP}}{h_{CP}} \end{cases}$$

Notice that in the case where $m_P > \frac{\alpha_{CP}}{h_{CP}}$, we get that $H_C > r_C$ since $r_C \left(1 + \frac{m_P}{e_{CP} K_C (m_P h_{CP} - \alpha_{CP})}\right) > r_C$. This contradicts the condition needed to have $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ be biologically relevant; namely that $H_C < r_C$. Thus, in order for the predators to be able to invade the system at $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$, we either need to have $H_C < r_C$ with $m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$ or $m_P < \frac{\alpha_{CP}}{h_{CP}}$ with $H_C < r_C \left(1 + \frac{m_P}{e_{CP} K_C (m_P h_{CP} - \alpha_{CP})}\right)$.

Biological Remark: If $m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$, the consumers can be harvested at a rate $H_C < r_C$, which is higher than the rate at which consumers can be harvested at in the case where $m_P < \frac{\alpha_{CP}}{h_{CP}}$. Likewise, if $m_P < \frac{\alpha_{CP}}{h_{CP}}$, the consumers can be harvested at a rate $H_C < r_C \left(1 + \frac{m_P}{e_{CP} K_C (m_P h_{CP} - \alpha_{CP})}\right)$, which is lower than the rate at which consumers can be harvested at in the case where $m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$. When the predators' natural mortality rate is not as large, which is the case when $m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}$, the predators do not need as much food to grow and invade so there can be more harvesting of the consumers. But when the predators'

natural mortality rate is larger, the predators need more food to be able to invade, so there cannot be as much harvesting of the consumers.

5.5.4   Invasion and Exclusion When the Resource is Absent

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) > 0$, invasibility condition (4.37) becomes

$$r_R > \cfrac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + e_{CP}h_{PC}\left[\cfrac{\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right)}{e_P h_P m_P}\right] + \frac{1}{2}e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C}$$
$$+ \frac{2e_{RP}\alpha_{CP}}{e_P h_P\left(\alpha_{CP} - h_{CP}m_P\right)} \tag{5.44}$$

and exclusion condition (4.38) becomes

$$r_R < \cfrac{\frac{1}{2}e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + \frac{e_{CP}^2 h_{PC}\alpha_{CP}}{e_P h_P m_P}\left(\frac{r_C - H_C}{r_C}\right)K_C + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C}$$
$$+ \cfrac{e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right)\right]}{e_P h_P m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) + \alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C}. \tag{5.45}$$

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) < 0$, invasibility condition (4.39)

$$r_R > \frac{e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + \frac{1}{2}e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C} + \frac{\frac{e_{RP}\left(\frac{r_C - H_C}{r_C}\right)K_C\alpha_{CP}e_{CP}}{e_P h_P m_P}}{1 + \frac{1}{2}e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C} \tag{5.46}$$

and exclusion condition (4.40) becomes

$$r_R < \frac{\frac{1}{2}e_{RC}\left(\frac{r_C - H_C}{r_C}\right)K_C}{1 + \frac{e_{CP}^2 h_{PC}\alpha_{CP}}{e_P h_P m_P}\left(\frac{r_C - H_C}{r_C}\right)K_C + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C}. \tag{5.47}$$

Before stating the following theorem, we introduce some terminology.

Definition 5.5.   *1. We say that increasing H_C makes it easier for the resource to invade if the right hand side of either invasibility condition (5.44) or (5.46) is a decreasing function of H_C; i.e., if increasing H_C reduces the minimum value of r_R necessary for the resource to invade. We say that increasing H_C makes it harder for the resource to invade if the right hand side of either invasibility condition (5.44) or (5.46) is an increasing function of H_C; i.e., if increasing H_C increases the minimum value of r_R necessary for the resource to invade.*

2. We say that increasing H_C makes it easier for the resource to be excluded if the right hand side of either exclusion condition (5.45) or (5.47) is an increasing function of H_C; i.e., if increasing H_C increases the maximum value of r_R, below which the resource will be excluded. We say that increasing H_C makes it harder for the resource to be excluded if the right hand side of either exclusion condition (5.45) or (5.47) is a decreasing function of H_C; i.e., if increasing H_C decreases the maximum value of r_R, below which the resource is excluded.

Theorem 5.14. *Increasing H_C*

1. makes invasion easier if

   (a) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) > 0$ and $e_{CP}h_{PC} < e_P h_P$.

   (b) $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) < 0$.

2. makes invasion harder if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) > 0$ and $e_{CP}h_{PC} > e_P h_P$.

3. makes exclusion harder.

Proof. The condition $\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) > 0$ is

equivalent to

$$
H_C \begin{cases} < r_C \left(1 - \dfrac{m_P}{e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - h_{CP}m_P\right)}\right) & \text{if } m_P < \frac{\alpha_{CP}}{2h_{CP}} \\[3mm] > r_C \left(1 - \dfrac{m_P}{e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - h_{CP}m_P\right)}\right) & \text{if } m_P > \frac{\alpha_{CP}}{2h_{CP}} \end{cases}
$$

Since we must have $H_C < r_C$, then we must have $H_C < r_C \left(1 - \dfrac{m_P}{e_{CP}K_C\left(\frac{1}{2}\alpha_{CP} - h_{CP}m_P\right)}\right)$ with $m_P < \frac{\alpha_{CP}}{2h_{CP}}$. Note that in order to ensure $H_C > 0$, we must have $m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$.

The second fraction on the right hand side of invasibility condition (5.44) is independent of H_C. The first fraction on the right hand side of invasibility condition (5.44) is of the form

$$
f(H_C) = \frac{A - BH_C}{C + DH_C}
$$

where

$$
\begin{aligned}
A &= e_{RC}K_C \\[2mm]
B &= \frac{e_{RC}K_C}{r_C} \\[2mm]
C &= 1 + e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)}{e_P h_P m_P}\right] + \frac{1}{2}e_C h_C K_C \\[2mm]
D &= e_{CP}h_{PC}\left(\frac{e_{CP}h_{CP}K_C}{r_C e_P h_P} - \frac{\alpha_{CP}e_{CP}K_C}{2r_C e_P h_P m_P}\right) - \frac{e_C h_C K_C}{2r_C}
\end{aligned}
$$

Here, both C and D could be either positive or negative. We have that

$$
f'(H_C) = -\frac{BC + AD}{(C + DH_C)^2} \begin{cases} > 0 \text{ if } D < -\frac{BC}{A} \\[3mm] < 0 \text{ if } D > -\frac{BC}{A} \end{cases}.
$$

Note that

$$D < -\frac{BC}{A} \Leftrightarrow e_{CP}h_{PC}\left(\frac{e_{CP}h_{CP}K_C}{r_Ce_Ph_P} - \frac{\alpha_{CP}e_{CP}K_C}{2r_Ce_Ph_Pm_P}\right) - \frac{e_Ch_CK_C}{2r_C}$$

$$< -\frac{\frac{e_{RC}K_C}{r_C}\left(1 + e_{CP}h_{PC}\left[\frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1+e_{CP}h_{CP}K_C)}{e_Ph_Pm_P}\right] + \frac{1}{2}e_Ch_CK_C\right)}{e_{RC}K_C}$$

$$\Leftrightarrow \frac{e_{CP}^2h_{CP}h_{PC}K_C}{r_Ce_Ph_P} - \frac{\alpha_{CP}e_{CP}^2h_{PC}K_C}{2r_Ce_Ph_Pm_P}$$

$$< -\frac{1}{r_C} - \frac{\alpha_{CP}e_{CP}^2h_{PC}K_C}{2r_Ce_Ph_Pm_P} + \frac{e_{CP}h_{PC}}{r_Ce_Ph_P} + \frac{e_{CP}^2h_{PC}h_{CP}K_C}{r_Ce_Ph_P}$$

$$0 < -\frac{1}{r_C} + \frac{e_{CP}h_{PC}}{r_Ce_Ph_P}$$

$$\Leftrightarrow e_Ph_P < e_{CP}h_{PC}$$

and

$$D > -\frac{BC}{A} \Leftrightarrow e_{CP}h_{PC} < e_Ph_P.$$

So, if $e_Ph_P < e_{CP}h_{PC}$ then increasing H_C causes the right hand side of invasibility condition to (5.44) increase. This makes invasion harder. But, if $e_{CP}h_{PC} < e_Ph_P$ then increasing H_C causes the right hand side of invasibility condition (5.44) to decrease. This makes invasion easier.

The first fraction on the right hand side of exclusion condition (5.45) is of the form

$$f(H_C) = \frac{A - BH_C}{C - DH_C}$$

where

$$A = \frac{1}{2}e_{RC}h_{RC}K_C$$
$$B = \frac{e_{RC}h_{RC}K_C}{2r_C}$$
$$C = 1 + \frac{e_{CP}^2h_{PC}\alpha_{CP}K_C}{e_Ph_Pm_P} + e_Ch_CK_C$$
$$D = \frac{e_{CP}^2h_{PC}\alpha_{CP}K_C}{e_Ph_Pm_Pr_C} + \frac{e_Ch_CK_C}{r_C}$$

We have that

$$f'(H_C) = \frac{AD - BC}{(C - DH_C)^2} \begin{cases} > 0 \text{ if } AD > BC \\ \\ < 0 \text{ if } AD < BC \end{cases}.$$

Note that

$$
\begin{aligned}
AD > BC &\Leftrightarrow \frac{1}{2}e_{RC}h_{RC}K_C \left(\frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{e_P h_P m_P r_C} + \frac{e_C h_C K_C}{r_C} \right) \\
&> \frac{e_{RC}h_{RC}K_C}{2r_C} \left(1 + \frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{e_P h_P m_P} + e_C h_C K_C \right) \\
&\Leftrightarrow \frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{e_P h_P m_P r_C} + \frac{e_C h_C K_C}{r_C} > \frac{1}{r_C} + \frac{e_{CP}^2 h_{PC}\alpha_{CP}K_C}{e_P h_P m_P r_C} + \frac{e_C h_C K_C}{r_C} \\
&\Leftrightarrow 0 > \frac{1}{r_C}
\end{aligned}
$$

and

$$AD < BC \Leftrightarrow 0 < \frac{1}{r_C}.$$

So, we must have that $f'(H_C) < 0$. Thus, increasing H_C causes the first fraction on the right hand side of exclusion condition (5.45) to decrease.

The second fraction on the right hand side of exclusion condition (5.45) is of the form

$$g(H_C) = \frac{A + BH_C}{C - DH_C}$$

where

$$
\begin{aligned}
A &= e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) \right] \\
B &= e_{RP}\left(-\frac{\alpha_{CP}e_{CP}K_C}{2r_C} + \frac{m_P e_{CP}h_{CP}K_C}{r_C} \right) \\
C &= e_P h_P m_P(1 + e_{CP}h_{CP}K_C) + \alpha_{CP}e_{CP}K_C \\
D &= \frac{e_P h_P m_P e_{CP}h_{CP}K_C}{r_C} + \frac{\alpha_{CP}e_{CP}K_C}{r_C}
\end{aligned}
$$

Here, A and B could be positive or negative. We have that

$$g'(H_C) = \frac{AD + BC}{(C - DH_C)^2} \begin{cases} > 0 \text{ if } AD > -BC \\ \\ < 0 \text{ if } AD < -BC \end{cases}.$$

Note that

$$
\begin{aligned}
AD > -BC \Leftrightarrow{} & e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)\right]\left(\frac{e_Ph_Pm_Pe_{CP}h_{CP}K_C}{r_C}\right. \\
& \left. + \frac{\alpha_{CP}e_{CP}K_C}{r_C}\right) \\
> {} & -e_{RP}\left(-\frac{\alpha_{CP}e_{CP}K_C}{2r_C} + \frac{m_Pe_{CP}h_{CP}K_C}{r_C}\right)[e_Ph_Pm_P(1 + e_{CP}h_{CP}K_C) \\
& + \alpha_{CP}e_{CP}K_C] \\
\Leftrightarrow{} & \left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)\right]\left(\frac{e_Ph_Pm_Pe_{CP}h_{CP}K_C}{r_C} + \frac{\alpha_{CP}e_{CP}K_C}{r_C}\right) \\
> {} & \left(\frac{\alpha_{CP}e_{CP}K_C}{2r_C} - \frac{m_Pe_{CP}h_{CP}K_C}{r_C}\right)(e_Ph_Pm_Pe_{CP}h_{CP}K_C + \alpha_{CP}e_{CP}K_C) \\
& + \left(\frac{\alpha_{CP}e_{CP}K_C}{2r_C} - \frac{m_Pe_{CP}h_{CP}K_C}{r_C}\right)e_Ph_Pm_P \\
\Leftrightarrow{} & 0 > e_Ph_pm_P\left(\frac{\alpha_{CP}e_{CP}K_C}{2r_C} - \frac{m_Pe_{CP}h_{CP}K_C}{r_C}\right) \\
\Leftrightarrow{} & \frac{1}{2}\alpha_{CP} < m_Ph_{CP}
\end{aligned}
$$

and

$$AD < -BC \Leftrightarrow \frac{1}{2}\alpha_{CP} > m_Ph_{CP}.$$

Since it is necessary to have $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ to be in this case, we have that increasing H_C causes the second fraction on the right hand side of exclusion condition (5.45) to decrease.

Thus, increasing H_C causes both the first and second fractions on the right hand side of exclusion condition (5.45) to decrease. So when we add these fractions together, we get that the right hand side of exclusion condition (5.45) is decreasing as a result of increasing H_C. This makes exclusion harder.

The condition $\frac{1}{2}\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) < 0$ is

equivalent to

$$
H_C \begin{cases} > r_C \left(1 - \dfrac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P \right)} \right) & \text{if } m_P < \dfrac{\alpha_{CP}}{2h_{CP}} \\[3mm] < r_C \left(1 - \dfrac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P \right)} \right) & \text{if } m_P > \dfrac{\alpha_{CP}}{2h_{CP}} \end{cases}
$$

Since we must have $H_C < r_C$, then in the case where $m_P > \frac{\alpha_{CP}}{2h_{CP}}$, we always have $H_C < r_C \left(1 - \dfrac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P \right)} \right)$. But if $m_P < \frac{\alpha_{CP}}{2h_{CP}}$ then we need to have $H_C > r_C \left(1 - \dfrac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P \right)} \right)$ in order to be in this case.

The first fraction on the right hand side of invasibility condition (5.46) is of the form

$$
f(H_C) = \frac{A - BH_C}{C - DH_C}
$$

where

$$
A = e_{RC} K_C
$$
$$
B = \frac{e_{RC} K_C}{r_C}
$$
$$
C = 1 + \frac{1}{2} e_C h_C K_C
$$
$$
D = \frac{e_C h_C K_C}{2r_C}
$$

We have that $f'(H_C) > 0$ if $AD > BC$ and $f'(H_C) < 0$ if $AD < BC$. Note that

$$
\begin{aligned}
AD > BC & \Leftrightarrow \frac{e_{RC} e_C h_C K_C^2}{2r_C} > \frac{e_{RC} K_C \left(\frac{1}{2} e_C h_C K_C \right)}{r_C} \\[2mm]
& \Leftrightarrow \frac{1}{2} e_C h_C K_C > 1 + \frac{1}{2} e_C h_C K_C \\[2mm]
& \Leftrightarrow 0 > 1
\end{aligned}
$$

and

$$
AD < BC \Leftrightarrow 0 < 1.
$$

So we have that increasing H_C causes the first fraction on the right hand side of invasibility condition (5.46) to decrease.

The second fraction on the right hand side of invasibility condition (5.46) is of the form

$$g(H_C) = \frac{E - F H_C}{G - I H_C}$$

where

$$E = \frac{e_{RP} K_C \alpha_{CP} e_{CP}}{e_P h_P m_P}$$

$$F = \frac{e_{RP} K_C \alpha_{CP} e_{CP}}{e_P h_P m_P r_C}$$

$$G = 1 + \frac{1}{2} e_{CP} h_{CP} K_C$$

$$I = \frac{e_{CP} h_{CP} K_C}{2 r_C}$$

We have that $g'(H_C) > 0$ if $EI > FG$ and $g'(H_C) < 0$ if $EI < FG$. Note that

$$EI > FG \Leftrightarrow \frac{e_{RP} K_C^2 \alpha_{CP} e_{CP}^2 h_{CP}}{2 r_C e_P h_P m_P} > \frac{e_{RP} K_C \alpha_{CP} e_{CP} \left(1 + \frac{1}{2} e_{CP} h_{CP} K_C\right)}{e_P h_P m_P r_C}$$

$$\Leftrightarrow \frac{1}{2} K_C e_{CP} h_{CP} > 1 + \frac{1}{2} e_{CP} h_{CP} K_C$$

$$\Leftrightarrow 0 > 1$$

and

$$EI < FG \Leftrightarrow 0 < 1.$$

So we have that increasing H_C causes the second fraction on the right hand side of invasibility condition (5.46) to decrease.

Thus, increasing H_C causes both the first and second fractions on the right hand side of invasibility condition (5.46) to decrease. When we add these fractions together, we get that the right hand side of invasibility condition (5.46) is decreasing, which makes invasion easier.

The right hand side of exclusion condition (5.47) is of the form

$$f(H_C) = \frac{A - BH_C}{C - DH_C}$$

where

$$A = \frac{1}{2} e_{RC} K_C$$

$$B = \frac{e_{RC} K_C}{2r_C}$$

$$C = 1 + \frac{e_{CP}^2 h_{PC} \alpha_{CP} K_C}{e_P h_P m_P} + e_C h_C K_C$$

$$D = \frac{e_{CP}^2 h_{PC} \alpha_{CP} K_C}{e_P h_P m_P r_C} + \frac{e_C h_C K_C}{r_C}$$

We have that $f'(H_C) > 0$ if $AD > BC$ and $f'(H_C) < 0$ if $AD < BC$. Note that

$$\begin{aligned} AD > BC &\Leftrightarrow \frac{1}{2} e_{RC} K_C \left(\frac{e_{CP}^2 h_{PC} \alpha_{CP} K_C}{e_P h_P m_P r_C} + \frac{e_C h_C K_C}{r_C} \right) \\ &> \frac{e_{RC} K_C}{2r_C} \left(1 + \frac{e_{CP}^2 h_{PC} \alpha_{CP} K_C}{e_P h_P m_P} + e_C h_C K_C \right) \\ &\Leftrightarrow 0 > 1 \end{aligned}$$

and

$$AD < BC \Leftrightarrow 0 < 1.$$

So we have that increasing H_C causes the right hand side of exclusion condition (5.47) to decrease, which makes exclusion harder. $\qquad \square$

5.5.5 Invasion and Exclusion When the Predators are Absent

In the case where $0 < R^* < K_R$ and $e_{RC}h_{RC}K_R < 1 + e_Ch_C\left(\frac{r_C - H_C}{r_C}\right)K_C$
$\Leftrightarrow H_C < r_C\left(1 + \frac{1 - e_{RC}h_{RC}K_R}{e_Ch_CK_C}\right)$, invasibility condition (4.54) becomes

$$m_P < \frac{\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C}{r_C\left(1 + e_Ch_C\left(\frac{r_C - H_C}{r_C}\right)K_C\right)\left(1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) + \beta} \tag{5.48}$$

where $\beta = \alpha_{RC}e_{RC}K_R e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C$, and exclusion condition (4.55) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C}$$

$$+ \frac{\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{(r_C - H_C)\left(1 + e_Ch_C\left(\frac{r_C - H_C}{r_C}\right)K_C\right)}\right)}{1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C}. \tag{5.49}$$

Note that if $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$, then we would have $H_C < 0$. So in order to be in this case, we must have $e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C$. In this case, the calculations and expressions become prohibitively long and complicated, and drawing useful conclusions becomes difficult. However, we can obtain useful information in some special cases. For instance, in the case where $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$, the first fraction on the right hand side of exclusion condition (5.49) dominates the second fraction so effectively, the exclusion condition becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C}. \tag{5.50}$$

Before stating the following theorem, we introduce some terminology.

Definition 5.6. *We say that increasing H_C makes it harder for the predators to be excluded if the right hand side of either exclusion condition (5.50) is an increasing function of H_C; i.e., if increasing H_C increases the minimum value of m_P which*

results in the predators being excluded.

Theorem 5.15. *Increasing H_C makes exclusion harder.*

Proof. In this case, the right hand side of exclusion condition (5.50) is of the form

$$f(H_C) = \frac{A}{B - CH_C}$$

where

$$A = \alpha_{RP} e_{RP} K_R$$

$$B = 1 + e_{CP} h_{PC} K_C$$

$$C = \frac{e_{CP} h_{PC} K_C}{r_C}$$

We have that $f'(H_C) > 0$. So when $\alpha_{RP} e_{RP} K_R >> \alpha_{CP} e_{CP} K_C$, increasing H_C causes the right hand side of exclusion condition (5.50) to increase. This makes exclusion harder. $\qquad\square$

In the case where $0 < R^* < K_R$ and $1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right) K_C < e_{RC} h_{RC} K_R \Leftrightarrow H_C > r_C \left(1 + \frac{1 - e_{RC} h_{RC} K_R}{e_C h_C K_C}\right)$, invasibility condition (4.56) becomes

$$m_P < \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C}{1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C \left(1 + \frac{\alpha_{RC}}{(r_C - H_C) h_{RC}}\right)} \tag{5.51}$$

and exclusion condition (4.57) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{CP} h_{PC} \left(\frac{r_C - H_C}{r_C}\right) K_C} + \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) \left(1 + \frac{\alpha_{RC}}{(r_C - H_C) h_{RC}}\right)}{1 + e_{CP} h_{CP} K_C}. \tag{5.52}$$

Note that if $1 + e_C h_C K_C < e_{RC} h_{RC} K_R$ then $1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right) K_C < e_{RC} h_{RC} K_R$ will always be satisfied. In this case, the calculations and expressions become prohibitively

long and complicated, and drawing useful conclusions becomes difficult. However, we can obtain useful information in some special cases. For instance, in the case where $\alpha_{RP}e_{RP}K_R \gg \alpha_{CP}e_{CP}K_C$, the first fraction on the right hand side of exclusion condition (5.52) dominates the second fraction so effectively, the exclusion condition becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C}.$$

which is the same as equation (5.50).

In the case where $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C \Leftrightarrow H_C < r_C\left(1 + \frac{1 - \frac{1}{2}e_{RC}h_{RC}K_R}{e_C h_C K_C}\right)$, invasibility condition (4.68) becomes

$$
\begin{aligned}
m_P < &\frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{(r_C - H_C)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C\right)}\right)} \\
&+ \frac{\alpha_{CP}e_{CP}K_C}{1 + e_{RP}h_{RP}K_R + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{(r_C - H_C)\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C\right)}\right)}
\end{aligned}
$$

$$(5.53)$$

and exclusion condition (4.69) becomes

$$
\begin{aligned}
m_P > &\frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C} \\
&+ \frac{\alpha_{CP}e_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\left(1 + \frac{\alpha_{RC}e_{RC}K_R}{r_C\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R + e_C h_C\left(\frac{r_C - H_C}{r_C}\right)K_C\right)}\right)}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C}
\end{aligned}
$$

$$(5.54)$$

Note that if $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}K_R$ then we would have $H_C < 0$. So we must have $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$ in order to be in this case. In this case, the calculations and expressions become prohibitively long and complicated, and drawing useful conclusions becomes difficult. However, we can obtain useful information in some special cases. For instance, in the case where $\alpha_{RP}e_{RP}K_R \gg \alpha_{CP}e_{CP}K_C$, the first fraction on the right hand side of the exclusion condition dominates the second

fraction so effectively, exclusion condition (5.54) becomes

$$m_P > \frac{\alpha_{RP}e_{RP}K_R}{1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}\left(\frac{r_C - H_C}{r_C}\right)K_C}. \tag{5.55}$$

Definition 5.7. *We say that increasing H_C makes it harder for the predators to be excluded if the right hand side of exclusion condition (5.55) is an increasing function of K_C; i.e., if increasing H_C increases the minimum value of m_P which results in the predators being excluded.*

Theorem 5.16. *Increasing H_C makes exclusion harder.*

Proof. The right hand side of exclusion condition (5.55) is of the form

$$f(H_C) = \frac{A}{B - CH_C}$$

where

$$A = \alpha_{RP}e_{RP}K_R$$
$$B = 1 + \frac{1}{2}e_{RP}h_{RP}K_R + e_{CP}h_{PC}K_C$$
$$C = \frac{e_{CP}h_{PC}K_C}{r_C}$$

We have that $f'(H_C) > 0$. So when $\alpha_{RP}e_{RP}K_R \gg \alpha_{CP}e_{CP}K_C$, increasing H_C causes the right hand side of exclusion condition (5.55) to increase. This makes exclusion harder. $\square$

In the case where $\frac{K_R}{2} < R^* < K_R$ and $1 + e_C h_C \left(\frac{r_C - H_C}{r_C}\right) K_C < \frac{1}{2}e_{RC}h_{RC}K_R \Leftrightarrow$

$H_C > r_C \left(1 + \frac{1 - \frac{1}{2} e_{RC} h_{RC} K_R}{e_C h_C K_C} \right)$, invasibility condition (4.72) becomes

$$m_P < \frac{\frac{1}{2} \alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R + e_{CP} h_{PC} \left(\frac{r_C - H_C}{r_C} \right) K_C \left(1 + \frac{\alpha_{RC}}{(r_C - H_C) h_{RC}} \right)}$$

$$+ \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C}{1 + e_{RP} h_{RP} K_R + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C \left(1 + \frac{\alpha_{RC}}{(r_C - H_C) h_{RC}} \right)} \qquad (5.56)$$

and exclusion condition (4.73) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} K_R}{1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C}$$

$$+ \frac{\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C \left(1 + \frac{\alpha_{RC}}{(r_C - H_C) h_{RC}} \right)}{1 + e_{CP} h_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C} \qquad (5.57)$$

Note that if $1 + e_C h_C K_C > \frac{1}{2} e_{RC} h_{RC} K_R$ then we get $H_C > 0$, which is always true. In this case, the calculations and expressions become prohibitively long and complicated, and drawing useful conclusions becomes difficult. However, we can obtain useful information in some special cases. For instance, in the case where $\alpha_{RP} e_{RP} K_R \gg \alpha_{CP} e_{CP} K_C$, the first fraction on the right hand side of exclusion condition (5.57) dominates the second fraction so effectively, the exclusion condition becomes

$$m_P > \frac{\alpha_{RP} e_{RP} K_R}{1 + \frac{1}{2} e_{RP} h_{RP} K_R + e_{CP} h_{PC} \left(\frac{r_C - H_C}{r_C} \right) K_C}.$$

This is the same as equation (5.55). So, we know that increasing H_C makes exclusion harder.

5.6 Harvesting the Predators in the Full Model

If we harvest only the predators, the form of the full model is

$$
\begin{aligned}
\frac{dR}{dt} &= r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P} \\
&\quad - \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} \\
\frac{dC}{dt} &= r_C C \left(1 - \frac{C}{K_C}\right) + \frac{\alpha_{RC} e_{RC} RC}{1 + e_{RC} h_{RC} R + e_C h_C C + e_{CP} h_{PC} P} \\
&\quad - \frac{e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} \\
\frac{dP}{dt} &= \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} + \frac{\alpha_{CP} e_{CP} CP}{1 + e_{RP} h_{RP} R + e_{CP} h_{CP} C + e_P h_P P} \\
&\quad - (m_P + H_P) P
\end{aligned}
\tag{5.58}
$$

5.6.1 Invasion and Exclusion When All Species are Absent

The eigenvalues of the Jacobian matrix at the equilibrium $(0, 0, 0)$ are

$$
\lambda_1 = r_R > 0
$$

$$
\lambda_2 = r_C > 0
$$

$$
\lambda_3 = -(m_P + H_P) < 0
$$

In this case, $(0, 0, 0)$ will be a saddle, with the resource and consumers able to invade and the predators being excluded.

5.6.2 Invasion and Exclusion When the Consumers and Predators are Absent

The eigenvalues of the Jacobian matrix at $(K_R, 0, 0)$ are

$$\lambda_1 = -r_R < 0$$

$$\lambda_2 = r_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R} > 0$$

$$\lambda_3 = -(m_P + H_P) + \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R}$$

In this case, the consumers will be able to invade the system at $(K_R, 0, 0)$. The predators will be able to invade the system if $\lambda_3 > 0 \Leftrightarrow H_P < -m_P + \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R}$.
Note that it is necessary to have $m_P < \frac{\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R}$ in order to have $H_P > 0$.

5.6.3 Invasion and Exclusion When the Resource and Predators are Absent

The eigenvalues of the Jacobian matrix at $(0, K_C, 0)$ are

$$\lambda_1 = r_R \left(1 - \frac{e_{RC} K_C}{1 + e_C h_C K_C} \right)$$

$$\lambda_2 = -r_C < 0$$

$$\lambda_3 = -(m_P + H_P) + \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$$

If $\lambda_1 > 0$ then the resource can invade the system at $(0, K_C, 0)$. But $\lambda_1 > 0 \Leftrightarrow 1 + e_C h_C K_C > e_{RC} K_C$. If $\lambda_3 > 0$ then the predators can invade the system at $(0, K_C, 0)$. But $\lambda_3 > 0 \Leftrightarrow H_P < -m_P + \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$. Note that in order to ensure $H_P > 0$, we must have $m_P < \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$.

5.6.4 Invasion and Exclusion When the Resource is Absent

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0 \Leftrightarrow H_P < -m_P + \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$, invasibility condition (4.37) becomes

$$r_R > \frac{e_{RC}K_C e_P h_P(m_P + H_P)}{e_P h_P(m_P + H_P)\left(1 + \frac{1}{2}e_C h_C K_C\right) + e_{CP}h_{PC}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C)\right]}$$
$$+ \frac{2e_{RP}\alpha_{CP}}{e_P h_P(\alpha_{CP} - h_{CP}(m_P + H_P))} \tag{5.59}$$

and exclusion condition (4.38) becomes

$$r_R < \frac{\frac{1}{2}e_{RC}K_C e_P h_P(m_P + H_P)}{(m_P + H_P)(1 + e_C h_C K_C) + e_{CP}^2 h_{PC}K_C\alpha_{CP}}$$
$$+ \frac{e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C)\right]}{e_P h_P(m_P + H_P)(1 + e_{CP}h_{CP}K_C) + K_C\alpha_{CP}e_{CP}} \tag{5.60}$$

Note that it is necessary to have $m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$ in order to have $H_P > 0$.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0 \Leftrightarrow H_P > -m_P + \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$, invasibility condition (4.39) becomes

$$r_R > \frac{e_{RC}K_C}{1 + \frac{1}{2}e_C h_C K_C} + \frac{e_{RP}K_C\alpha_{CP}e_{CP}}{e_P h_P(m_P + H_P)\left(1 + \frac{1}{2}e_{CP}h_{CP}K_C\right)} \tag{5.61}$$

and exclusion condition (4.40) becomes

$$r_R < \frac{\frac{1}{2}e_{RC}K_C e_P h_P(m_P + H_P)}{e_P h_P(m_P + H_P)(1 + e_C h_C K_C) + e_{CP}^2 h_{PC}K_C\alpha_{CP}}. \tag{5.62}$$

Note that if $m_P > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$, then we will be in the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$ for any level of harvesting of the predator.

Before stating the following theorem, we introduce some terminology.

Definition 5.8. *1. We say that increasing H_P makes it easier for the resource to invade if the right hand side of either invasibility condition (5.59) or (5.61) is a decreasing function of H_P; i.e., if increasing H_P reduces the minimum value*

of r_R necessary for the resource to invade. We say that increasing H_P makes it harder for the resource to invade if the right hand side of either invasibility condition (5.59) or (5.61) is an increasing function of H_P; i.e., if increasing H_P increases the minimum value of r_R necessary for the resource to invade.

2. *We say that increasing H_P makes it easier for the resource to be excluded if the right hand side of either exclusion condition (5.60) or (5.62) is an increasing function of H_P; i.e., if increasing H_P increases the maximum value of r_R, below which the resource will be excluded. We say that increasing H_P makes it harder for the resource to be excluded if the right hand side of either exclusion condition (5.60) or (5.62) is a decreasing function of H_P; i.e., if increasing H_P decreases the maximum value of r_R, below which the resource is excluded.*

Theorem 5.17. *Increasing H_P*

1. *makes invasion easier if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$.*

2. *makes invasion harder if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$.*

3. *makes exclusion easier if*

   (a) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} \gg e_{RP}$.*

   (b) *$\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$.*

4. *makes exclusion harder if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} \ll e_{RP}$.*

Proof. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$, the first fraction on the right hand side of invasibility condition (5.59) is of the form

$$f(H_P) = \frac{A + BH_P}{C + DH_P}$$

where

$$A = e_{RC}K_C e_P h_P m_P$$

$$B = e_{RC}K_C e_P h_P$$

$$C = e_P h_P m_P \left(1 + \frac{1}{2}e_C h_C K_C\right) + \frac{1}{2}\alpha_{CP}e_{CP}^2 h_{PC}K_C - e_{CP}h_{CP}m_P(1 + e_{CP}h_{PC}K_C)$$

$$D = e_P h_P \left(1 + \frac{1}{2}e_C h_C K_C\right) - e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)$$

Here, D could be positive or negative, but $C > 0$. To see this, note that in order to be in this case, we had the condition $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$ which implies that $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$. But $e_P h_P m_P \left(1 + \frac{1}{2}e_C h_C K_C\right) + \frac{1}{2}\alpha_{CP}e_{CP}^2 h_{PC}K_C - e_{CP}h_{CP}m_P(1 + e_{CP}h_{PC}K_C) > \frac{1}{2}\alpha_{CP}e_{CP}^2 h_{PC}K_C - e_{CP}h_{CP}m_P(1 + e_{CP}h_{PC}K_C) = e_{CP}h_{CP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{PC}K_C)\right] > 0$. We have that

$$f'(H_P) = \frac{BC - AD}{(C + DH_P)^2} \begin{cases} > 0 \text{ if } D < \frac{BC}{A} \\ < 0 \text{ if } D > \frac{BC}{A} \end{cases}.$$

Note that

$$D > \frac{BC}{A} \Leftrightarrow e_P h_P \left(1 + \frac{1}{2}e_C h_C K_C\right) - e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)$$

$$< \frac{e_{RC}K_C e_P h_P}{e_{RC}K_C e_P h_P m_P}\left[e_P h_P m_P \left(1 + \frac{1}{2}e_C h_C K_C\right) + \frac{1}{2}\alpha_{CP}e_{CP}^2 h_{PC}K_C\right.$$

$$\left. - e_{CP}h_{PC}m_P(1 + e_{CP}h_{CP}K_C)\right]$$

$$\Leftrightarrow e_P h_P \left(1 + \frac{1}{2}e_C h_C K_C\right) - e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)$$

$$< e_P h_P \left(1 + \frac{1}{2}e_C h_C K_C\right) + \frac{\alpha_{CP}e_{CP}^2 h_{PC}K_C}{2m_P} - e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)$$

$$\Leftrightarrow 0 < \frac{\alpha_{CP}e_{CP}^2 h_{PC}K_C}{2m_P}$$

and

$$D < \frac{BC}{A} \Leftrightarrow 0 > \frac{\alpha_{CP} e_{CP}^2 h_{PC} K_C}{2m_P}.$$

So, we have that $f'(H_P) > 0$. Thus, increasing H_P causes the first fraction on the right hand side of invasibility condition (5.59) to increase.

The second fraction on the right hand side of invasibility condition (5.59) is of the form

$$g(H_P) = \frac{A}{B - CH_P}$$

where

$$A = 2e_{RP}\alpha_{CP}$$

$$B = e_P h_P (\alpha_{CP} - h_{CP} K_C m_P)$$

$$C = e_P h_P h_{CP}$$

We have that $g'(H_P) > 0$ so increasing H_P causes the second fraction on the right hand side of invasibility condition (5.59) to increase.

Thus, increasing H_P causes both the first and second fractions on the right hand side of invasibility condition (5.59) to increase. When we add these fractions together, we get that the right hand side of invasibility condition (5.59) is increasing. So, increasing H_P makes invasion harder.

The first fraction on the right hand side of exclusion condition (5.60) is of the form

$$f(H_P) = \frac{A + BH_P}{C + DH_P}$$

where

$$A = \frac{1}{2} e_{RC} K_C e_P h_P m_P$$

$$B = \frac{1}{2} e_{RC} K_C e_P h_P$$

$$C = m_P(1 + e_C h_C K_C) + e_{CP}^2 h_{PC} K_C \alpha_{CP}$$

$$D = 1 + e_C h_C K_C$$

We have that $f'(H_P) > 0$ if $BC > AD$ and $f'(H_P) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \frac{1}{2} e_{RC} K_C e_P h_P \left[m_P(1 + e_C h_C K_C) + e_{CP}^2 h_{PC} K_C \alpha_{CP} \right]$$

$$> \frac{1}{2} e_{RC} K_C e_P h_P m_P(1 + e_C h_C K_C)$$

$$\Leftrightarrow m_P(1 + e_C h_C K_C + e_{CP}^2 h_{PC} K_C \alpha_{CP} > m_P(1 + e_C h_C K_C)$$

$$\Leftrightarrow e_{CP}^2 h_{PC} K_C \alpha_{CP} > 0$$

and

$$BC < AD \Leftrightarrow e_{CP}^2 h_{PC} K_C \alpha_{CP} < 0.$$

Thus, we have that $f'(H_P) > 0$. So, increasing H_P causes the first fraction on the right hand side of exclusion condition (5.60) to increase.

The second fraction on the right hand side of exclusion condition (5.60) is of the form

$$g(H_P) = \frac{A - BH_P}{C + DH_P}$$

where

$$A = e_{RP}\left[\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C)\right]$$

$$B = e_{RP}(1 + e_{CP}h_{CP}K_C)$$

$$C = e_{Ph_P}m_P(1 + e_{CP}h_{CP}K_C) + K_C\alpha_{CP}e_{CP}$$

$$D = e_{Ph_P}(1 + e_{CP}h_{CP}K_C)$$

As noted above, $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ so here, $A > 0$. We have that

$$g'(H_P) = -\frac{BC + AD}{(C + DH_P)^2} < 0.$$

So increasing H_P causes the second fraction on the right hand side of exclusion condition (5.60) to decrease.

Thus, increasing H_P causes the first fraction on the right hand side of exclusion condition (5.60) to increase, while causing the second fraction to decrease. When we add these fractions together, we get that the right hand side of exclusion condition (5.60) could be increasing or decreasing as a result of increasing H_P. If $e_{RC} >> e_{RP}$ then the first fraction on the right hand side of exclusion condition (5.60) dominates the second fraction. In this case, increasing H_P causes the right hand side of exclusion condition (5.60) to increase, which makes exclusion easier. But if $e_{RC} << e_{RP}$ then the second fraction on the right hand side of exclusion condition (5.60) dominates the first fraction. In this case, increasing H_P causes the right hand side of exclusion condition (5.60) to decrease, which makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$, the first fraction on the right hand side of invasibility condition (5.61) is independent of H_P. The second fraction on the right hand side of the invasibility condition is of the form

$$f(H_P) = \frac{A}{B + CH_P}$$

where

$$A = e_{RP} K_C \alpha_{CP} e_{CP}$$

$$B = e_P h_P m_P \left(1 + \frac{1}{2} e_{CP} h_{CP} K_C \right)$$

$$C = e_P h_P \left(1 + \frac{1}{2} e_{CP} h_{CP} K_C \right)$$

We have that $f'(H_P) < 0$ so increasing H_P causes the right hand side of invasibility condition (5.61) to decrease. This makes invasion easier.

The right hand side of exclusion condition (5.62) is of the form

$$f(H_P) = \frac{A + B H_P}{C + D H_P}$$

where

$$A = \frac{1}{2} e_{RC} K_C e_P h_P m_P$$

$$B = \frac{1}{2} e_{RC} K_C e_P h_P$$

$$C = e_P h_P m_P (1 + e_C h_C K_C) + e_{CP}^2 h_{PC} K_C \alpha_{CP}$$

$$D = e_P h_P (1 + e_C h_C K_C)$$

We have that $f'(H_P) > 0$ if $BC > AD$ and $f'(H_P) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \frac{1}{2} e_{RC} K_C e_P h_P \left[e_P h_P m_P (1 + e_C h_C K_C) + e_{CP}^2 h_{PC} K_C \alpha_{CP} \right]$$

$$> \frac{1}{2} e_{RC} K_C e_P^2 h_P^2 m_P (1 + e_C h_C K_C)$$

$$\Leftrightarrow e_P h_P m_P (1 + e_C h_C K_C) + e_{CP}^2 h_{PC} K_C \alpha_{CP} > e_P h_P m_P (1 + e_C h_C K_C)$$

$$\Leftrightarrow e_{CP}^2 h_{PC} K_C \alpha_{CP} > 0$$

and

$$BC < AD \Leftrightarrow e_{CP}^2 h_{PC} K_C \alpha_{CP} < 0.$$

Thus, $f'(H_P) > 0$. So increasing H_P causes the right hand side of exclusion condition (5.61) to increase, which makes exclusion easier. $\qquad\square$

5.6.5 Invasion and Exclusion When the Consumers are Absent

In the case where $\frac{1}{2}\alpha_{RP} e_{RP} K_R - (m_P + H_P)(1 + h_{RP} e_{RP} K_R) > 0 \Leftrightarrow H_P < \frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R} - m_P$, invasibility condition (4.46) becomes

$$r_C > \frac{2 e_{CP} \alpha_{RP}}{e_P h_P (\alpha_{RP} - (m_P + H_P) h_{RP})} \\ - \frac{\frac{1}{2} e_P h_P \alpha_{RC} e_{RC} K_R (m_P + H_P)}{e_P h_P (m_P + H_P)(1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}} \tag{5.63}$$

and exclusion condition (4.47) becomes

$$r_C < \frac{e_{CP}\left[\frac{1}{2} e_{RP} \alpha_{RP} K_R - (m_P + H_P)(1 + e_{RP} h_{RP} K_R)\right]}{e_P h_P (m_P + H_P) e_{RP} h_{RP} K_R + e_P h_P K_R \alpha_{RP} e_{RP}} \\ - \frac{e_P h_P \alpha_{RC} e_{RC} K_R (m_P + H_P)}{e_P h_P (m_P + H_P)\left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) + e_{CP} h_{CP}\left[\frac{1}{2}\alpha_{RP} e_{RP} K_R - (m_P + H_P)(1 + e_{RP} h_{RP} K_R)\right]} \tag{5.64}$$

Note that in this case, it is necessary to have $m_P < \frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R}{1 + h_{RP} e_{RP} K_R}$ in order to have $H_P > 0$.

In the case where $\frac{1}{2}\alpha_{RP} e_{RP} K_R - (m_P + H_P)(1 + h_{RP} e_{RP} K_R) < 0 \Leftrightarrow H_P > \frac{\frac{1}{2}\alpha_{RP} e_{RP} K_R}{1 + e_{RP} h_{RP} K_R} - m_P$, invasibility condition (4.48) becomes

$$r_C > \frac{e_{CP} K_R \alpha_{RP} e_{RP}}{e_P h_P (m_P + H_P)\left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)} \\ - \frac{\frac{1}{2} e_P h_P \alpha_{RC} e_{RC} K_R (m_P + H_P)}{e_P h_P (m_P + H_P)(1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}} \tag{5.65}$$

and exclusion condition (4.49) becomes

$$r_C < -\frac{\alpha_{RC}e_{RC}K_R}{1 + \frac{1}{2}e_{RC}h_{RC}K_R}. \tag{5.66}$$

Note that if $m_P > \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1+e_{RP}h_{RP}K_R}$ then we will be in this case for any level of predator harvesting, H_P. Also note that in this case, the consumers cannot be excluded from the system.

Before stating the following theorem, we introduce some terminology.

Definition 5.9. *1. We say that increasing H_P makes it easier for the consumers to invade if the right hand side of either invasibility condition (5.63) or (5.65) is a decreasing function of H_P; i.e., if increasing H_P reduces the minimum value of r_C necessary for the consumers to invade. We say that increasing H_P makes it harder for the consumers to invade if the right hand side of either invasibility condition (5.63) or (5.65) is an increasing function of H_P; i.e., if increasing H_P increases the minimum value of r_C necessary for the consumers to invade.*

2. We say that increasing H_P makes it easier for the consumers to be excluded if the right hand side of either exclusion condition (5.64) or (5.66) is an increasing function of H_P; i.e., if increasing H_P increases the maximum value of r_C, below which the consumers will be excluded. We say that increasing H_P makes it harder for the consumers to be excluded if the right hand side of either exclusion condition (5.64) or (5.66) is a decreasing function of H_P; i.e., if increasing H_P decreases the maximum value of r_C, below which the consumers is excluded.

Theorem 5.18. *Increasing H_P*

1. makes invasion easier if

   (a) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) > 0$ and $e_{CP}\alpha_{RP} << \alpha_{RC}e_{RC}$.

   (b) $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) < 0$.

2. *makes invasion harder if* $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) > 0$ *and*

$e_{CP}\alpha_{RP} >> \alpha_{RC}e_{RC}$.

3. *makes exclusion harder if* $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) > 0$.

Proof. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) > 0$, the first fraction on the right hand side of invasion condition (5.63) is of the form

$$f(H_P) = \frac{A}{B - CH_P}$$

where

$$A = 2e_{CP}\alpha_{RP}$$

$$B = e_P h_P(\alpha_{RP} - m_P h_{RP}K_R)$$

$$C = e_P h_P h_{RP}$$

Here, $B > 0$. To see this, note that to be in this case, it was necessary that $m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1+e_{RP}h_{RP}K_R} \Leftrightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R > m_P(1 + e_{RP}h_{RP}K_R)$. But $\frac{1}{2}\alpha_{RP}e_{RP}K_R > m_P(1 + e_{RP}h_{RP}K_R) \Rightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R > m_P e_{RP}h_{RP}K_R \Leftrightarrow \frac{1}{2}\alpha_{RP} > m_P h_{RP}K_R \Rightarrow \alpha_{RP} > m_P h_{RP}K_R$. We have that $f'(H_P) > 0$ so increasing H_P causes the first fraction on the right hand side of invasibility condition (5.63) to increase.

The second fraction on the right hand side of invasibility condition (5.63) is of the form

$$g(H_P) = \frac{A + BH_P}{C + DH_P}$$

where

$$A = \frac{1}{2}e_P h_P \alpha_{RC} e_{RC} K_R m_P$$

$$B = \frac{1}{2}e_P h_P \alpha_{RC} e_{RC} K_R$$

$$C = e_P h_P m_P (1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}$$

$$D = e_P h_P (1 + e_{RC} h_{RC} K_R)$$

We have that $g'(H_P) > 0$ if $BC > AD$ and $g'(H_P) < 0$ if $BC < AD$. Note that

$$BC > AD \Leftrightarrow \frac{1}{2}e_P h_P \alpha_{RC} e_{RC} K_R \left[e_P h_P m_P (1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} \right]$$

$$> \frac{1}{2}e_P^2 h_P^2 \alpha_{RC} e_{RC} K_R m_P (1 + e_{RC} h_{RC} K_R)$$

$$\Leftrightarrow e_P h_P m_P (1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP}$$

$$> e_P h_p m_P (1 + e_{RC} h_{RC} K_R)$$

$$\Leftrightarrow e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} > 0$$

and

$$BC < AD \Leftrightarrow e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} < 0.$$

So we have that $g'(H_P) > 0$. Thus, increasing H_P causes the second fraction on the right hand side of invasibility condition (5.63) to increase.

So, increasing H_P causes both the first and second fraction on the right hand side of invasibility condition (5.63) to increase. But when we subtract the second fraction from the first fraction, we get that the right hand side of invasibility condition (5.63) could be increasing or decreasing as a result of increasing H_P. If $e_{CP}\alpha_{RP} >>$ $\alpha_{RC} e_{RC}$ then the first fraction on the right hand side of invasibility condition (5.63) dominates the second fraction. In this case, increasing H_P causes the right hand side of invasibility condition (5.63) to increase, which makes invasion harder. But, if

$e_{CP}\alpha_{RP} << \alpha_{RC}e_{RC}$ then the second fraction on the right hand side of invasibility condition (5.63) dominates the first fraction. In this case, increasing H_P causes the right hand side of invasibility condition (5.63) to decrease, which makes invasion easier.

The first fraction on the right hand side of exclusion condition (5.64) is of the form

$$f(H_P) = \frac{A - BH_P}{C + DH_P}$$

where

$$A = e_{CP}\left[\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P(1 + e_{RP}h_{RP}K_R)\right]$$

$$B = e_{CP}(1 + e_{RP}h_{RP}K_R)$$

$$C = e_{Ph}h_P m_P e_{RP}h_{RP}K_R + e_{Ph}PK_R\alpha_{RP}e_{RP}$$

$$D = e_{Ph}p e_{RP}h_{RP}K_R$$

As noted above, it is necessary to have $\frac{1}{2}\alpha_{RP}e_{RP}K_R > m_P(1 + e_{RP}h_{RP}K_R)$ in order to be in this case. Thus, we must have $A > 0$. We have that

$$f'(H_P) = -\frac{BC + AD}{(C + DH_P)^2} < 0.$$

So, increasing H_P causes the first fraction on the right hand side of exclusion condition (5.64) to decrease.

The second fraction on the right hand side of exclusion condition (5.64) is of the form

$$g(H_P) = \frac{A + BH_P}{C + DH_P}$$

where

$$A = e_P h_P \alpha_{RC} e_{RC} K_R m_P$$

$$B = e_P h_P \alpha_{RC} e_{RC} K_R$$

$$C = e_P h_P m_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) + e_{CP} h_{CP} \left[\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + e_{RP} h_{RP} K_R)\right]$$

$$D = e_P h_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) - e_{CP} h_{CP}(1 + e_{RP} h_{RP} K_R)$$

Since it is necessary to have $\frac{1}{2}\alpha_{RP} e_{RP} K_R > m_P(1 + e_{RP} h_{RP} K_R)$ to be in this case, we have that $C > 0$. But, D could be positive or negative. We have that $g'(H_P) > 0$ if $D < \frac{BC}{A}$ and $g'(H_P) < 0$ if $D > \frac{BC}{A}$. Note that

$$\begin{aligned}
D < \frac{BC}{A} &\Leftrightarrow e_P h_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) - e_{CP} h_{CP}(1 + e_{RP} h_{RP} K_R) \\
&< \frac{e_P h_P \alpha_{RC} e_{RC} K_R}{e_P h_P \alpha_{RC} e_{RC} K_R m_P}\left(e_P h_P m_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right)\right. \\
&\quad + \left. e_{CP} h_{CP} \left[\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + e_{RP} h_{RP} K_R)\right]\right) \\
&\Leftrightarrow e_P h_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) - e_{CP} h_{CP}(1 + e_{RP} h_{RP} K_R) \\
&< e_P h_P \left(1 + \frac{1}{2} e_{RC} h_{RC} K_R\right) + \frac{\alpha_{RC} e_{RP} e_{CP} h_{CP} K_R}{2 m_P} \\
&\quad - e_{CP} h_{CP}(1 + e_{RP} h_{RP} K_R) \\
&\Leftrightarrow 0 < \frac{\alpha_{RC} e_{RP} e_{CP} h_{CP} K_R}{2 m_P}
\end{aligned}$$

and

$$D > \frac{BC}{A} \Leftrightarrow 0 > \frac{\alpha_{RC} e_{RP} e_{CP} h_{CP} K_R}{2 m_P}.$$

So we have that $g'(H_P) > 0$. Thus, increasing H_P causes the second fraction on the right hand side of exclusion condition (5.64) to increase.

So, increasing H_P causes the first fraction on the right hand side of exclusion

condition (5.64) to decrease, while causing the second fraction to increase. When we subtract the second fraction from the first fraction, we get that the right hand side of exclusion condition (5.64) is decreasing as a result of increasing H_P. This makes exclusion harder.

In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + h_{RP}e_{RP}K_R) < 0$, the first fraction on the right hand side of invasibility condition (5.65) is of the form

$$f(H_P) = \frac{A}{B + CH_P}$$

where

$$A = e_{CP}K_R\alpha_{RP}e_{RP}$$
$$B = e_Ph_Pm_P\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$
$$C = e_Ph_P\left(1 + \frac{1}{2}e_{RC}h_{RC}K_R\right)$$

We have that $f'(H_P) < 0$ so increasing H_P causes the first fraction on the right hand side of invasibility condition (5.65) to decrease.

The second fraction on the right hand side of invasibility condition (5.65) is of the form

$$g(H_P) = \frac{A + BH_P}{C + DH_P}$$

where

$$A = \frac{1}{2}e_Ph_P\alpha_{RC}e_{RC}K_Rm_P$$
$$B = \frac{1}{2}e_Ph_P\alpha_{RC}e_{RC}K_R$$
$$C = e_Ph_Pm_P(1 + e_{RC}h_{RC}K_R) + e_{CP}h_{CP}K_R\alpha_{RP}e_{RP}$$
$$D = e_Ph_P(1 + e_{RC}h_{RC}K_R)$$

We have that $g'(H_P) > 0$ if $BC > AD$ and $g'(H_P) < 0$ if $BC < AD$. Note that

$$
\begin{aligned}
BC > AD \Leftrightarrow & \frac{1}{2} e_{Ph_P} \alpha_{RC} e_{RC} K_R \left[e_{Ph_P} m_P (1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} \right] \\
& > \frac{1}{2} e_P^2 h_P^2 \alpha_{RC} e_{RC} K_R m_P (1 + e_{RC} h_{RC} K_R) \\
& \Leftrightarrow e_{Ph_P} m_P (1 + e_{RC} h_{RC} K_R) + e_{CP} h_{CP} K_E \alpha_{RP} e_{RP} \\
& > e_{Ph_P} m_P (1 + e_{RC} h_{RC} K_R) \\
& \Leftrightarrow e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} > 0
\end{aligned}
$$

and

$$
BC < AD \Leftrightarrow e_{CP} h_{CP} K_R \alpha_{RP} e_{RP} < 0.
$$

So we have that $g'(H_P) > 0$. Thus, increasing H_P causes the second fraction on the right hand side of invasibility condition (5.65) to increase.

So, increasing H_P causes the first fraction on the right hand side of the invasibility condition to decrease, while causing the second fraction to increase. When we subtract an increasing fraction from a decreasing fraction, we get that the right hand side of the invasibility condition is decreasing. This makes invasion easier. $\qquad \square$

Chapter 6

Special Cases

6.1 Linear Food Chain without Harvesting

If $e_{RP} = 0$ in (2.18), then the predators do not attack the resource. This gives us the linear food chain (2.15).

The eigenvalues of the Jacobian matrix at $(0,0,0)$ do not change.

At $(K_R, 0, 0)$, eigenvalues λ_1 and λ_2 do not change. But we end up with $\lambda_3 = -m_P$.

Biological Remark: In the case of intraguild predation, the predator could invade at $(K_R, 0, 0)$ under certain conditions. But now, the predators do not consume the resource, so the predators have no food source. So the predators are now excluded from the system at $(K_R, 0, 0)$. Despite this, the system can still be permanent since the consumers can still invade the system at $(K_R, 0, 0)$.

At $(0, K_C, 0)$, all the eigenvalues remain the same as the case of intraguild predation.

Biological Remark: Since the resource and predators are absent from the system at $(0, K_C, 0)$, it does not matter whether or not the resource is part of the predators' diet. The resource and predators will be able to invade or will be excluded from the system the same as in intraguild predation.

At $\left(0, C^*, P^*\right)$, the resource invasibility condition (4.35) becomes

$$r_R > \frac{e_{RC}C^*}{1 + e_{CP}h_{PC}P^* + e_C h_C C^*}$$

and the resource exclusion condition (4.36) becomes

$$r_R < \frac{e_{RC}C^*}{1 + e_{CP}h_{PC}P^* + e_C h_C C^*}.$$

This condition is weaker than the case of intraguild predation, which means that it is easier for the basal resource to invade and harder to be excluded.

Biological Remark: It makes sense that it would be easier for the resource to invade and harder for the basal resource to be excluded from a linear food chain than a system with intraguild predation. One reason this makes sense is that the basal resource has one less species feeding upon it, which makes it easier for the basal resource to grow. Another is that by not feeding upon the basal resource, the predators have more time to allot to preying upon the consumers. This will depress the consumer population further than if the predators fed upon both the basal resource and consumers. Fewer consumers feeding upon the basal resource also makes it easier for the basal resource to grow.

At $\left(R^*, 0, P^*\right)$, the consumer invasibility condition (4.43) becomes

$$r_C > \frac{e_{CP}P^*}{1 + e_P h_P P^*} - \frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^* + e_{CP}h_{CP}P^*} \tag{6.1}$$

and the consumer exclusion condition (4.43) becomes

$$r_C > \frac{e_{CP}P^*}{1 + e_P h_P P^*} - \frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^* + e_{CP}h_{CP}P^*}. \tag{6.2}$$

But in a linear food chain, if the consumer is absent, then $P^* = 0$, so invasibility

condition (6.1) becomes

$$r_C > -\frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^*}$$

and exclusion condition (6.2) becomes

$$r_C < -\frac{\alpha_{RC}e_{RC}R^*}{1 + e_{RC}h_{RC}R^*}.$$

This shows that the consumer will always be able to invade and can never be excluded.

Biological Remark: Because $P^* = 0$ in a linear food chain when $C^* = 0$, the only source of predation mortality for the consumer is absent. So the consumers are free to grow and establish themselves.

At $\left(R^*, C^*, 0\right)$, the predator invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{CP}h_{CP}C^*}$$

and the predator exclusion condition (4.53)

$$m_P > \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{CP}h_{CP}C^*}.$$

These conditions cannot be compared directly to the case of intraguild predation, without more information about the parameters. On the one hand, the predator has one less food source, which should have a negative impact on the predators' ability to grow. But it also means the consumers have less competition for food so they can grow more. This means more food for the predators from consuming the consumers. More specifically, if the predator gains more from consuming the basal resource than the consumers in the case of intraguild predation, then losing the basal resource as a food source makes it harder for the predator to invade. Therefore, the invasibility condition becomes stronger. On the other hand, if the predator gains more from consuming the consumers, then losing the basal resource makes it easier for the predator to invade,

so the invasibility condition becomes weaker.

To see this, let's rewrite (4.52) as

$$m_P < \alpha_{RP} \left(\frac{e_{RP}R^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \frac{\frac{\alpha_{CP}}{\alpha_{RP}}e_{CP}C^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{CP}C^*} \right). \quad (6.3)$$

We can see that if $\alpha_{RP} >> \alpha_{CP}$ then the second term is small so (6.3) becomes

$$m_P < \frac{\alpha_{RP}e_{RP}R^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \varepsilon \quad (6.4)$$

for ε small. So now, if $e_{RP} = 0$ because we have a linear food chain, then we get that

$$m_P < \varepsilon.$$

So it is harder for the predator to invade because its mortality rate must be very small. Similarly, we could rewrite (4.52) as

$$m_P < \alpha_{CP} \left(\frac{\frac{\alpha_{RP}}{\alpha_{CP}}e_{RP}R^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \frac{e_{CP}C^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{CP}C^*} \right). \quad (6.5)$$

We can see that if $\alpha_{CP} >> \alpha_{RP}$ then the first term is small so (6.5) becomes

$$m_P < \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{RP}h_{RP}R^* + e_{CP}h_{PC}C^*} + \varepsilon \quad (6.6)$$

for ε small. So now, if $e_{RP} = 0$ because we have a linear food chain, then we get that

$$m_P < \frac{\alpha_{CP}e_{CP}C^*}{1 + e_{CP}h_{CP}C^*} + \varepsilon.$$

In this case, m_P can be larger than in the case of intraguild predation (since the fraction on the righthand side has a smaller denominator) so the condition is weaker. This makes it easier for the predator to invade in this case.

We could rewrite (4.53) similarly to see that exclusion will be easier if $\alpha_{RP} >> \alpha_{CP}$ and harder if $\alpha_{RP} << \alpha_{CP}$.

6.2 Linear Food Chain with Harvesting

6.2.1 Harvesting the Resource

At $(0,0,0)$, the only species whose invasibility condition is different than in the unharvested case is the resource. In this case, we need $H_R < r_R$ in order for the resource to be able to invade.

We need $H_R < r_R$ in order for $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0, 0\right)$ to be biologically relevant. If this is the case, then λ_3 remains the same as in the unharvested case, but λ_1 and λ_2 change. We now end up with $\lambda_1 = H_R - r_R$ and $\lambda_2 = r_C + \frac{\alpha_{RP} e_{RP}\left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R}$. Since $H_R < r_R$, we have $\lambda_1 < 0$ and $\lambda_2 > 0$. So the invasibility and exclusion of each species at $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0, 0\right)$ does not change between the unharvested case and the harvested case.

At $(0, K_C, 0)$, λ_2 and λ_3 remain the same as the unharvested case. But λ_1 now becomes $\lambda_1 = (r_R - H_R)\left(1 - \frac{e_{RC} K_C}{1 + e_C h_C K_C}\right)$. This is the same as the case of intraguild predation with harvesting.

The interior equilibrium $\left(R^*, 0, P^*\right)$ does not exist in a linear food chain because $P^* = 0$ if $C^* = 0$.

At $\left(0, C^*, P^*\right)$, harvesting the resource makes it harder for the resource to invade and easier for the resource to be excluded.

At $\left(R^*, C^*, 0\right)$, in the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$, we see from inequalities (5.34) - (5.37) and Theorem 5.11 that when $e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R < 1 + e_C h_C K_C$, harvesting the resource makes it easier for the predators to invade and easier for them to be excluded. We also see that harvesting the resource has no effect on the invasibility or exclusion of the predators when $1 + e_C h_C K_C < e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R$.

At $\left(R^*, C^*, 0\right)$, in the case where $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $\frac{1}{2} e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R < 1 + e_C h_C K_C$, we could not analyze the effects of harvesting except in a special case. But since $e_{RP} = 0$ in a linear food chain, we can see that the right hand side of invasibility condition (5.38) is increasing in H_R and the right hand side of exclusion condition (5.39) is decreasing in H_R. Therefore, increasing H_R makes it easier for the predators to invade and easier for the predators to be excluded from the system in this case.

In the case where $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R$, setting $e_{RP} = 0$ in invasibility condition (5.41) and exclusion condition (5.42) results in the right hand side of each inequality being independent of H_R. So in this case, harvesting the resource has no effect on the invasibility or exclusion of the predators.

6.2.2   Harvesting the Consumers

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the consumer. In this case, we need $H_C < r_C$ in order for the consumers to be able to invade.

At $(K_R, 0, 0)$, λ_1 and λ_3 remain the same as the unharvested case. But λ_2 now becomes $\lambda_2 = r_C - H_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$. This is the same as the case of intraguild predation with harvesting.

We need $H_C < r_C$ in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ to be biologically relevant. If this is the case then invasibility and exclusion are the same as in the case of intraguild predation.

We still cannot have the interior equilibrium $\left(R^*, 0, P^*\right)$ since $P^* = 0$ when $C^* = 0$.

At $\left(0, C^*, P^*\right)$, if we set $e_{RP} = 0$ in consumer invasibility and exclusion conditions (5.44) - (5.47) and use Theorem 5.14, we see that increasing H_C makes invasion easier and exclusion harder.

At $\left(R^*, C^*, 0\right)$ in the case of intraguild predation, the best we could do was consider a special case because the expressions and calculations are prohibitively complicated otherwise. Unfortunately, having a linear food chain does not simplify the expressions or calculations sufficiently enough to make more progress.

6.2.3 Harvesting the Predators

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the predator. In both cases, however, the predators will be excluded from the system.

At $(K_R, 0, 0)$, λ_1 and λ_2 remain the same as in the unharvested case, but λ_3 changes. We now end up with $\lambda_3 = -(m_P + H_P) < 0$. So the predator will still be excluded from the system, just as in the unharvested case.

At $(0, K_C, 0)$, λ_1 and λ_2 remain the same as the unharvested case. But λ_3 now becomes $\lambda_3 = -(m_P + H_P) + \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$. This is the same as the case of intraguild predation.

We still cannot have the interior equilibrium $\left(R^*, 0, P^*\right)$ because $P^* = 0$ if $C^* = 0$.

At $\left(0, C^*, P^*\right)$, in the case where $\frac{1}{2}\alpha_{CP} e_{CP} K_C - (m_P + H_P)(1 + e_{CP} h_{CP} K_C) > 0$, we can see from invasibility condition (5.59), exclusion condition (5.60), and Theorem 5.17 that increasing H_P makes invasion harder and exclusion easier. In the case where $\frac{1}{2}\alpha_{CP} e_{CP} K_C - (m_P + H_P)(1 + e_{CP} h_{CP} K_C) < 0$, when we set $e_{RP} = 0$, the right hand side of invasibility condition (5.61) is independent of H_P and the right hand side of exclusion condition (5.62) is the same as in the case of intraguild predation.

At $\left(R^*, C^*, 0\right)$, harvesting the predators makes it harder for the predators to invade and easier for the predators to be excluded.

6.3 Apparent Competition Between the Resource and Consumers without Harvesting

If $e_{RC} = 0$ in (2.18) then the consumers do not attack the resource. This gives us the apparent competition model (2.16).

The eigenvalues of the Jacobian matrix at $(0, 0, 0)$ do not change.

At $(K_R, 0, 0)$, the eigenvalues of the Jacobian matrix all remain the same. In particular, the consumers will always be able to invade and the predators will be able to invade if inequality (4.31) holds.

Biological Remark: At $(K_R, 0, 0)$, there are no predators in the system so the consumers do not have any predation mortality. And since the consumers grow logistically in the absence of any other species, the consumers do not need the resource in order to grow. So in both intraguild predation and apparent competition, the consumers have nothing to stop them from invading. Also in both cases, the only food source available to the invading predators at $(K_R, 0, 0)$ is the resource. And the predator-prey relationship between the predators and resource is the same in both cases, so the invasibility condition for the predators is the same in both cases.

At $(0, K_C, 0)$, eigenvalues λ_2 and λ_3 remain the same. But λ_1 changes and invasibility condition (4.32) becomes

$$0 < \frac{r_R}{K_C} \left(1 + e_C h_C K_C \right).$$

This condition shows that the resource will always be able to invade.

Biological Remark: In apparent competition, the only predation threat to the resource comes from the predators. But at $(0, K_C, 0)$, the predators are absent so there is nothing to stop the resource from invading.

At $\left(0, C^*, P^*\right)$, the resource invasibility condition (4.35) becomes

$$r_R > \frac{e_{RP}P^*}{1 + e_{CP}h_{CP}C^* + e_Ph_PP^*}$$

and the resource exclusion condition (4.36) becomes

$$r_R < \frac{e_{RP}P^*}{1 + e_{CP}h_{CP}C^* + e_Ph_PP^*}.$$

These conditions are weaker than in the case of intraguild predation, which makes it easier for the resource to invade and harder for them to be excluded.

Biological Remark: It makes sense that it would be easier for the resource to invade and harder for them to be excluded. One reason is that the basal resource has one less species feeding upon it, which helps the resource to grow. Another reason is that the consumers will not have the extra food source so the size of its population will be depressed. A lower consumer population density means less food for the predators who are the basal resource's only enemy now. Thus, there will be fewer predators to prey upon the basal resource, which also makes it easier for the basal resource to grow.

At $\left(R^*, 0, P^*\right)$, the consumer invasibility condition (4.43) becomes

$$r_C > \frac{e_{CP}P^*}{1 + e_{RP}h_{RP}R^* + e_Ph_PP^*}$$

and the consumer exclusion condition (4.44) becomes

$$r_C < \frac{e_{CP}P^*}{1 + e_{RP}h_{RP}R^* + e_Ph_PP^*}.$$

These conditions are stronger than in the case of intraguild predation, which makes it harder for the consumer to invade and easier for them to be excluded.

Biological Remark: Since the consumers do not feed upon the resource in apparent

competition, it makes sense that it would be harder for them to invade the system and easier for them to be excluded from the system at $\left(R^*, 0, P^*\right)$. This is because now, one of the consumer's food sources is absent from its diet.

At $\left(R^*, C^*, 0\right)$, the predator invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*} + \frac{\alpha_{CP} e_{CP} C^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{CP} C^*}$$

and the predator exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*} + \frac{\alpha_{CP} e_{CP} C^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{CP} C^*}.$$

These conditions are the same as in the case of intraguild predation. This makes sense because in either case, the predator has both the basal resource and the predator to feed upon as it tries to invade.

6.4 Apparent Competition Between the Resource and Consumers with Harvesting

6.4.1 Harvesting the Resource

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the resource. In this case, we need $H_R < r_R$ in order for the resource to be able to invade.

We need $H_R < r_R$ in order for $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0, 0\right)$ to be biologically relevant. If this is the case, then λ_2 remains the same as in the unharvested case, but λ_1 and λ_3 change. We now end up with $\lambda_1 = H_R - r_R$ and $\lambda_3 = -m_P + \frac{\alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{RP} h_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}$. We have $\lambda_1 < 0$ just as in the unharvested case. We also have that λ_3 is the same in intraguild predation.

At $(0, K_C, 0)$, λ_2 and λ_3 are the same as the unharvested case. But λ_1 now becomes $\lambda_1 = r_R - H_R$. If $H_R < r_R$ then the resource will be able to invade the system. If $H_R > r_R$ then the resource will be excluded from the system.

At $(R^*, 0, P^*)$, we see from inequalities (5.30) - (5.33) and Theorem 5.10 that harvesting the resource makes it harder for the consumers to invade. Also, in the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R\right) > 0$, harvesting the resource makes it harder for the consumers to be excluded while in the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R\right) < 0$, harvesting the resource makes it easier for the consumers to be excluded from the system.

At $(0, C^*, P^*)$, harvesting the resource makes it harder for the resource to invade and easier for the resource to be excluded.

At $(R^*, C^*, 0)$, when $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right)K_R$, we cannot be in the case where $1 + e_C h_C K_C < e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R$ since $e_{RC} = 0$ in apparent competition and this would give us $1 + e_C h_C K_C < 0$. We can see from invasibility condition (5.34), exclusion condition (5.35), and Theorem 5.11 that increasing H_R makes it easier for the predators to invade and makes it easier for the predators to be excluded from the system.

In the case where $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right)K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right)K_R$, we cannot have the case where $1 + e_C h_C K_C < \frac{1}{2}e_{RC}h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R$ because $e_{RC} = 0$ in apparent competition and this would give us $1 + e_C h_C K_C < 0$. In the case where we had $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C$ in the intraguild predation model, we could not analyze the effects of harvesting except in a special case. But since $e_{RC} = 0$ in apparent competition, we can see that the first fraction on the right hand side of both invasibility condition (5.38) and exclusion condition (5.39) is decreasing in H_R while the second fractions in both are increasing. Thus, when we add these fractions together, we get that the right hand side of invasibility condition (5.38) and exclusion condition (5.39) could be increasing or decreasing. If $\alpha_{RP}e_{RP} \gg \alpha_{CP}e_{CP}$ then the first fraction on the right

hand side of invasibility condition (5.38) and exclusion condition (5.39) dominates the second fraction. In this case, increasing H_R causes the right hand side to decrease which makes invasion harder and exclusion easier. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side of invasibility condition (5.38) and exclusion condition (5.39) dominates the first fraction. In this case, increasing H_R causes the right hand side to increase which makes invasion easier and exclusion harder.

6.4.2   Harvesting the Consumers

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the consumer. In this case, we need $H_C < r_C$ in order for the resource to be able to invade.

At $(K_R, 0, 0)$, λ_1 and λ_3 remain the same as the unharvested case. But λ_2 now becomes $r_C - H_C$ which is positive if $H_C < r_C$.

We need $H_C < r_C$ in order for $\left(0, \left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$ to be biologically relevant. If this is the case then λ_2 and λ_3 are the same as in intraguild predation. But now $\lambda_1 = r_R > 0$.

At $(0, C^*, P^*)$, we can see that in the case where $\frac{1}{2} \alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C - m_P \left(1 + e_{RC} h_{RC} \left(\frac{r_C - H_C}{r_C} \right) K_C \right) > 0$, invasibility condition (5.44), exclusion condition (5.45), and Theorem 5.14 give us that invasibility is independent of H_C and exclusion is harder as a result of increasing H_C. In the case where $\frac{1}{2} \alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C} \right) K_C - m_P \left(1 + e_{RC} h_{RC} \left(\frac{r_C - H_C}{r_C} \right) K_C \right) < 0$, we can see from invasibility condition (5.46), exclusion condition (5.47), and Theorem 5.14 that increasing H_C makes invasion easier and exclusion harder.

At $(R^*, 0, P^*)$, harvesting the consumers makes it harder for the consumers to invade and easier for the consumers to be excluded.

In apparent competition, $(R^*, C^*, 0) = \left(K_R, \left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$. Thus, in order for this equilibrium to be biologically relevant, we must have $H_C < r_C$. In the

case where $0 < R^* < K_R$, we cannot have the case where we $1 + e_C h_C K_C < e_{RC} h_{RC} \left(\frac{r_C - H_C}{r_C} \right) K_C$. Since $e_{RC} = 0$ in apparent competition, this condition is equivalent to $H_C > r_C \left(1 + \frac{1}{e_C h_C K_C} \right) > r_C$. So we must be in the case where $e_{RC} h_{RC} K_R < 1 + e_C h_C \left(\frac{r_C - H_C}{r_C} \right) K_C$. We were not able to analyze this case in the intraguild predation model. But by setting $e_{RC} = 0$, we can see that the right hand side of invasibility condition (5.48) is decreasing in H_C. This makes invasion harder. Similarly, we can see that the first fraction on right hand side of exclusion condition (5.49) is increasing in H_C while the second fraction is decreasing. When we add these fractions together, we get that the right hand side of exclusion condition (5.49) could be increasing or decreasing as a result of increasing H_C. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the first fraction on the right hand side of exclusion condition (5.49) is increasing as a result of increasing H_C. This makes exclusion harder. But if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the second fraction on the right hand side of exclusion condition (5.49) dominates the first fraction. In this case, increasing H_C causes the right hand side to decrease. This makes exclusion easier.

6.4.3 Harvesting the Predators

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the predator. In both cases, however, the predators will be excluded from the system.

At $(K_R, 0, 0)$, λ_1 and λ_2 remain the same as in the unharvested case. We now end up with $\lambda_3 = -(m_P + H_P) < 0$. So the predator will still be excluded from the system, just as in the unharvested case.

At $(0, K_C, 0)$, λ_1 and λ_2 remain the same as in the unharvested case. But λ_3 now becomes $\lambda_3 = -(m_P + H_P) + \frac{\alpha_{CP} e_{CP} K_C}{1 + e_{CP} h_{CP} K_C}$. This is the same as the case of intraguild predation.

At $\left(0, C^*, P^* \right)$, in the case where $\frac{1}{2} \alpha_{CP} e_{CP} K_C - (m_P + H_P)(1 + e_{CP} h_{CP} K_C) > 0$,

invasibility condition (5.59), exclusion condition (5.60), and Theorem 5.17 give us that increasing H_P makes invasion harder and exclusion harder. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$, invasibility condition (5.61), exclusion condition (5.62), and Theorem 5.17 give us that the resource cannot be excluded and increasing H_P makes invasion easier.

At $\left(R^*, 0, P^*\right)$, in the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) > 0$, invasibility condition (5.63), exclusion condition (5.64), and Theorem 5.18 give us that increasing H_P makes invasion harder and exclusion harder. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) < 0$, invasibility condition (5.65), exclusion condition (5.66), and Theorem 5.18 give us that the predators cannot be excluded, although the exclusion condition is independent of H_P, and increasing H_P makes invasion easier.

At $\left(R^*, C^*, 0\right)$, increasing H_P makes it harder for the predators to invade and easier for them to be excluded.

6.5   Resource Competition without Harvesting

If $e_{CP} = 0$ in (2.18), then the predators do not attack the consumers. This gives us the resource competition model (2.17).

The eigenvalues of the Jacobian matrix at $(0, 0, 0)$ do no change.

At $(K_R, 0, 0)$, the eigenvalues of the Jacobian matrix do not change. In particular, predator invasibility condition (4.31) remains the same as the case of intraguild predation.

Biological Remark: Since the consumers and predators are absent from the system at $(K_R, 0, 0)$, it does not matter whether or not the consumers are part of the predators' diet. When the predators are absent, the consumers will be free of predation in intraguild predation just the same as they are in the case of resource competition. Similarly, when the consumers are absent, the predators will need to rely exclusively

on consuming the resource to invade in intraguild predation just the same as if the consumers were not part of their diet.

At $(0, K_C, 0)$, eigenvalues λ_1 and λ_2 remain the same, but λ_3 changes. This means that predator invasibility condition (4.32) becomes

$$0 > m_P.$$

This condition shows that the predator cannot invade.

Biological Remark: In the case of intraguild predation, the predator could invade $(0, K_C, 0)$ under certain conditions. But now, the predators do not consume the consumers, so predators have no food source. So the predators are now excluded from the system at $(0, K_C, 0)$.

At $(0, C^*, P^*)$, the resource invasibility condition (4.35) becomes

$$r_R > \frac{e_{RC}C^*}{1 + e_C h_C C^*} + \frac{e_{RP}P^*}{1 + e_P h_P P^*} \tag{6.7}$$

and the resource exclusion condition (4.36) becomes

$$r_R < \frac{e_{RC}C^*}{1 + e_C h_C C^*} + \frac{e_{RP}P^*}{1 + e_P h_P P^*}. \tag{6.8}$$

But in resource competition, if the resource is absent, then $P^* = 0$ and $C^* = K_C$, so the resource invasibility condition (6.7) becomes

$$r_R > \frac{e_{RC}K_C}{1 + e_C h_C K_C}$$

and the resource exclusion condition (6.8) becomes

$$r_R < \frac{e_{RC}K_C}{1 + e_C h_C K_C}.$$

These conditions cannot be compared directly to the case of intraguild predation without more information about the parameters. On the one hand, the consumers now have no predators so their population density will be higher. This means more consumers to feed upon the basal resource. On the other hand, the predators have one less food source so their population density will be lower. This means fewer predators to feed upon the basal resource. More specifically, if the consumers attack the basal resource more than the predators do in the case of intraguild predation, then not having the predators feed upon the consumers means more consumers to feed upon the basal resource, which would make it harder for the basal resource to invade. Therefore, the invasibility condition becomes stronger. On the other hand, if the predator attacks the basal resource more than the consumers do then not having the predators feed upon the consumers means fewer predators to feed upon the basal resource. This would make it easier for the basal resource to invade, so the invasibility condition becomes weaker.

To see this, let's rewrite (4.35) as

$$r_R > e_{RC} \left(\frac{C^*}{1 + e_{CP} h_{PC} P^* + e_C h_C C^*} + \frac{\frac{e_{RP}}{e_{RC}} P^*}{1 + e_{CP} h_{CP} C^* + e_P h_P P^*} \right). \tag{6.9}$$

We can see that if $e_{RC} >> e_{RP}$ then the second term is small so (6.9) becomes

$$r_R > \frac{e_{RC} C^*}{1 + e_{CP} h_{PC} P^* + e_C h_C C^*} + \varepsilon \tag{6.10}$$

for ε small. So now, if $e_{CP} = 0$ because we have resource competition, then we get

$$r_R > \frac{e_{RC} C^*}{1 + e_C h_C C^*} + \varepsilon.$$

So it is harder for the basal resource to invade because its intrinsic growth rate must be larger than in the case of intraguild predation (since the fraction on the righthand side

has a smaller denominator). Thus, the invasibility condition is stronger. Similarly, we could rewrite (4.35) as

$$r_R > e_{RP} \left(\frac{\frac{e_{RC}}{e_{RP}} C^*}{1 + e_{CP} h_{PC} P^* + e_C h_C C^*} + \frac{P^*}{1 + e_{CP} h_{CP} C^* + e_P h_P P^*} \right). \qquad (6.11)$$

We can see that if $e_{RP} >> e_{RC}$ then the first term is small so (6.11) becomes

$$r_R > \varepsilon + \frac{e_{RP} P^*}{1 + e_{CP} h_{CP} C^* + e_P h_P P^*} \qquad (6.12)$$

for ε small. So now, if $e_{CP} = 0$ because we have resource competition, then we get

$$r_R > \varepsilon.$$

In this case, r_R doesn't have to be as large as in the case of intraguild predation so the invasibility condition is weaker. This makes it easier for the basal resource to invade.

At $\left(R^*, 0, P^* \right)$, the consumer invasibility condition (4.43) becomes

$$r_C > -\frac{\alpha_{RC} e_{RC} R^*}{1 + e_{RC} h_{RC} R^*}$$

and the consumer exclusion condition (4.44) becomes

$$r_C < -\frac{\alpha_{RC} e_{RC} R^*}{1 + e_{RC} h_{RC} R^*}.$$

This shows that the consumer will always be able to invade and will never be excluded.

Biological Remark: It makes sense that at $\left(R^*, 0, P^* \right)$ the consumers will always be able to invade and will never be excluded. This is because the consumers have no source of predation mortality in resource competition so there is nothing to stop

them from growing.

At $\left(R^*, C^*, 0\right)$, the predator invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^*}$$

and the predator exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^*}.$$

These conditions cannot be compared directly to the case of intraguild predation without more information about the parameters. The possible negative impact on the predator by not feeding upon the consumers is clearly that the predator has one less food source to help its population grow as it tries to invade. But the possible positive impact on the predator is not so obvious. To see how resource competition might be more advantageous than intraguild predation for the invading predator, let us rewrite (4.52) as

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*} + \frac{\frac{\alpha_{CP}}{h_{CP}} e_{CP} C^*}{\frac{1}{h_{CP}} + \frac{e_{RP} h_{RP}}{h_{CP}} R^* + e_{CP} C^*}. \tag{6.13}$$

If $\frac{\alpha_{CP}}{h_{CP}} << 1$ then the second term is small so (6.13) becomes

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*} + \varepsilon \tag{6.14}$$

for ε small. So now, if $e_{CP} = 0$ because we have resource competition, then we get

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^*} + \varepsilon. \tag{6.15}$$

The fraction on the righthand side is larger than in (6.14). This means m_P can be larger than before and the predator will still be able to invade. This makes it easier

for the predator to invade. So if $\frac{\alpha_{CP}}{h_{CP}} \ll 1$ then the consumer not being part of the predator's diet is more advantageous for the invading predator than if the consumer were part of the predator's diet.

Biological Remark: This says that if the predator does not gain sufficiently from consuming the consumers compared to the time it spends handling consumers, then the predators are better off leaving the consumers alone and not wasting their time feeding upon them. Instead, they should feed solely on the basal resource.

6.6   Resource Competition with Harvesting

6.6.1   Harvesting the Resource

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the un-harvested case is the resource. In this case, we need $H_R < r_R$ in order for the resource to be able to invade.

At $\left(\left(\left(\frac{r_R - H_R}{r_R} \right) K_R, 0, 0 \right) \right.$, the eigenvalues of the Jacobian matrix are the same as in the case of intraguild predation with harvesting.

At $(0, K_C, 0)$, λ_2 and λ_3 remain the same as the unharvested case. But λ_1 now becomes $\lambda_1 = (r_R - H_R) \left(1 - \frac{e_{RC} K_C}{1 + e_C h_C K_C} \right)$. This is the same as the case of intraguild predation with harvesting.

The interior equilibrium $\left(0, C^*, P^* \right)$ is not possible in resource competition because $P^* = 0$ if $R^* = 0$.

At $\left(R^*, 0, P^* \right)$, we already have that the consumers can always invade and can never be excluded. Harvesting the resource does not change this, as the consumers do not need the resource to grow.

At $\left(R^*, C^*, 0 \right)$, in the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R} \right) K_R$, inequalities (5.34) - (5.37) along with Theorem 5.11 give us that the predators cannot invade the system and increasing H_R makes exclusion easier.

In the case where $\frac{1}{2}\left(\frac{r_R-H_R}{r_R}\right)K_R < R^* < \left(\frac{r_R-H_R}{r_R}\right)K_R$, inequalities (5.38) - (5.42) along with Theorem 5.13 give us that increasing H_R makes invasion harder and exclusion easier.

6.6.2 Harvesting the Consumers

At $(0,0,0)$, the only species whose invasibility condition is different than in the un-harvested case is the consumer. In this case, we need $H_C < r_C$ in order for the consumers to be able to invade.

At $(K_R,0,0)$, the eigenvalues of the Jacobian matrix are the same as in the case of intraguild predation with harvesting.

At $\left(0,\left(\frac{r_C-H_C}{r_C}\right)K_C,0\right)$, λ_3 remains the same as the unharvested case, but λ_1 and λ_2 change. We now have $\lambda_1 = r_R - \frac{e_{RC}(r_C-H_C)K_C}{r_C+e_Ch_C(r_C-H_C)K_C}$ and $\lambda_2 = H_C - r_C$. These are the same as in the case of intraguild predation.

The interior equilibrium $\left(0,C^*,P^*\right)$ is still not possible since $R^* = 0$ implies that $P^* = 0$.

At $\left(R^*,0,P^*\right)$, the consumers cannot be excluded and can always invade. But harvesting the consumers makes invasion harder and exclusion easier.

At $\left(R^*,C^*,0\right)$, in the case where $0 < R^* < K_R$, inequalities (5.48) - (5.52) give us that the predators cannot invade the system and exclusion condition is independent of H_C. In the case where $\frac{1}{2}K_R < R^* < K_R$, inequalities (5.53) - (5.57) give us that the invasibility and exclusion conditions are independent of H_C.

6.6.3 Harvesting the Predators

At $(0,0,0)$, the only species whose invasibility condition is different than in the un-harvested case is the predator. In both cases, however, the predators will be excluded from the system.

At $(K_R, 0, 0)$, the eigenvalues of the Jacobian matrix are the same as in the case of intraguild predation with harvesting.

At $(0, K_C, 0)$, λ_1 and λ_2 remain the same as in the unharvested case. But now $\lambda_3 = -(m_P + H_P)$. In this case, the predators will be excluded, just as they were in the unharvested case.

The interior equilibrium $(0, C^*, P^*)$ is still not possible since $R^* = 0$ implies that $P^* = 0$.

At $(R^*, 0, P^*)$, we already have that the consumers can always invade and can never be excluded. Harvesting the predators does not change this, as harvesting the predators increases R^* and decreases P^*.

At $(R^*, C^*, 0)$, harvesting the predators makes invasion harder and exclusion easier.

6.7 Interspecific Killing without Harvesting

If $\alpha_{CP} = 0$ in (2.18), then the predators attack but do not feed upon the consumers. This gives us interspecific killing. The eigenvalues of the Jacobian matrix at $(0, 0, 0)$ and $(K_R, 0, 0)$ do not change.

At $(0, K_C, 0)$, eigenvalues λ_1 and λ_2 do not change. But we end up with $\lambda_3 = -m_P$.

Biological Remark: In the case of intraguild predation, the predator could invade $(0, K_C, 0)$ under certain conditions. But now, the predators do not consume the consumers despite attacking them. So, the predators have no food source and are therefore excluded from the system at $(0, K_C, 0)$.

The interior equilibrium $(0, C^*, P^*)$ does not exist in this case because $P^* = 0$ if $R^* = 0$.

At $(R^*, 0, P^*)$, the consumer invasibility condition (4.43) and the consumer exclusion condition (4.44) remain the same.

Biological Remark: This makes sense because the attack rate on the consumers

is remaining the same whether we have interspecific killing or intraguild predation. So there is no difference to the consumers who are either invading or trying to avoid exclusion.

At $\left(R^*, C^*, 0\right)$, the predator invasibility condition (4.52) becomes

$$m_P < \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*}$$

and the predator exclusion condition (4.53) becomes

$$m_P > \frac{\alpha_{RP} e_{RP} R^*}{1 + e_{RP} h_{RP} R^* + e_{CP} h_{PC} C^*}.$$

These conditions are stronger than in the case of intraguild predation, which means that it is harder for the predators to invade and easier to be excluded.

Biological Remark: It makes sense that it would be harder for the predators to invade and easier for them to be excluded because the predators now have one less food source.

6.8 Interspecific Killing with Harvesting

6.8.1 Harvesting the Resource

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the resource. In this case, we need $H_R < r_R$ in order for the resource to be able to invade.

We need $H_R < r_R$ in order for $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0, 0\right)$ to be biologically relevant. If this is the case, then we end up with $\lambda_1 = H_R - r_R < 0$, $\lambda_2 = r_C + \frac{\alpha_{RC} e_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{RC} h_{RC} \left(\frac{r_R - H_R}{r_R}\right) K_R}$, and $\lambda_3 = -m_P + \frac{\alpha_{RP} e_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}{1 + e_{RP} h_{RP} \left(\frac{r_R - H_R}{r_R}\right) K_R}$. These are the same as the case of intraguild predation with harvesting.

At $(0, K_C, 0)$, λ_2 and λ_3 remain the same as in the unharvested case. But λ_1 now becomes $\lambda_1 = (r_R - H_R)\left(1 - \frac{e_{RC} K_C}{1 + e_C h_C K_C}\right)$. This is the same as the case of intraguild predation with harvesting.

The interior equilibrium $\left(0, C^*, P^*\right)$ does not exist in interspecific killing because $P^* = 0$ if $R^* = 0$.

At $\left(R^*, 0, P^*\right)$, inequalities (5.30) - (5.33) remain the same in the case of interspecific killing as in intraguild predation.

At $\left(R^*, C^*, 0\right)$, in the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$, we see from inequalities (5.34) - (5.37) and Theorem 5.11 that when $\alpha_{CP} = 0$, the predators cannot invade the system and increasing H_R makes it easier for the predators to be excluded.

6.8.2 Harvesting the Consumers

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the consumer. In this case, we need $H_C < r_C$ in order for the consumers to be able to invade.

At $(K_R, 0, 0)$, λ_1 and λ_3 remain the same as the unharvested case. But λ_2 now becomes $\lambda_2 = r_C - H_C + \frac{\alpha_{RC} e_{RC} K_R}{1 + e_{RC} h_{RC} K_R}$. This is the same as the case of intraguild predation with harvesting.

We need $H_C < r_C$ in order for $\left(0, \left(\frac{r_C - H_C}{r_C}\right) K_C, 0\right)$ to be biologically relevant. If this is the case then λ_3 remains the same as in the unharvested case while λ_1 and λ_2 are the same as the case of intraguild predation with harvesting.

The interior equilibrium $\left(0, C^*, P^*\right)$ does not exist in interspecific killing because $P^* = 0$ if $R^* = 0$.

At $\left(R^*, 0, P^*\right)$, harvesting the consumers makes it harder for the consumers to invade and easier for the consumers to be excluded.

At $\left(R^*, C^*, 0\right)$, in the case where $0 < R^* < K_R$, inequalities (5.48) - (5.52) and Theorem 5.15 give us that the predators cannot invade the system and increasing H_C

makes it harder for the predators to be excluded. In the case where $\frac{1}{2}K_R < R^* < K_R$, inequalities (5.53) - (5.57) and Theorem 5.16 give us that the invasibility conditions are still prohibitively complicated and increasing H_C makes it harder for the predators to be excluded.

6.8.3   Harvesting the Predators

At $(0, 0, 0)$, the only species whose invasibility condition is different than in the unharvested case is the predator. In both cases, however, the predators will be excluded.

At $(K_R, 0, 0)$, the eigenvalues of the Jacobian matrix are the same as in the case of intraguild predation with harvesting.

At $(0, K_C, 0)$, λ_1 and λ_2 remain the same as in the unharvested case. But now $\lambda_3 = -(m_P + H_P)$. In this case, the predators will be excluded, just as they were in the unharvested case.

The interior equilibrium $\left(0, C^*, P^*\right)$ does not exist in interspecific killing because $P^* = 0$ when $R^* = 0$.

At $\left(R^*, 0, P^*\right)$, the invasibility and exclusion conditions remain the same as the case of intraguild predation with harvesting.

At $\left(R^*, C^*, 0\right)$, harvesting the predators makes it harder for the predators to invade and easier for them to be excluded.

Chapter 7

More Biological Remarks and Discussion

7.1 Biological Remarks on Invasibility and Exclusion when Resource Absent

7.1.1 Increasing $e_C h_C$

According to Theorem 4.3, if

$$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$$

then increasing $e_C h_C$ makes it easier for the resource to invade and harder for them to be excluded.

If

$$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) < 0$$

then increasing $e_C h_C$ makes it easier for the resource to invade and harder for them to be excluded.

Biological Remark: Under any set of circumstances, the more the consumers interfere with each other, the easier it is for the resource to invade the system when they are absent. This is to be expected because the more the consumers interfere with

each other, the less they are preying upon the invading resource. Likewise, under any set of circumstances, the more the consumers interfere with each other, the harder it is for the resource to be excluded from the system. This is to be expected. The more the consumers interfere with each other, the less they are preying upon the resource. This, in turn, reduces the consumers' growth rate so there are less consumers to prey upon the resource. Having fewer consumers also reduces the predator's growth rate, which means fewer predators feeding upon the resource.

7.1.2 Increasing K_C

According to Theorem 4.4, if

$$m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_C > \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}, \ e_{CP}h_{PC} > e_P h_P$$

then increasing K_C makes it easier for the resource to invade. If any of

$$m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_C > 0$$

or

$$m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_C < \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}$$

or

$$m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_C > \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}, \ e_{CP}h_{PC} < e_P h_P$$

hold, then increasing K_C makes it harder for the resource to invade.

Biological Remark: For most parameter values, increasing K_C makes invasion harder. This is to be expected because increasing K_C means more consumers to feed upon the invading resource. It also means more food for the predators. This leads to more predators to also feed upon the invading resource. But, when $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_C > \frac{m_P}{\frac{1}{2}\alpha_{CP}e_{CP} - m_P e_{CP}h_{CP}}, \ e_{CP}h_{PC} > e_P h_P$, the predators are sufficiently efficient in gaining from feeding upon the consumers compared to the time they spend

handling encountered consumers. The predator mortality rate and their intraspecific interference is also sufficiently low. Thus, there is not much to limit the predators' growth rate. But, in this case, the consumers spend a sufficiently large amount of time avoiding predators. Increasing K_C increases the amount of food available for predators, which increases the number of predators. This, in turn, means the consumers will spend even more time avoiding predators. This leaves less time for consuming the resource. Additionally, if the consumers spend a large amount of time avoiding predators, the predators might need to spend more time searching for consumers to feed upon, even if they do not spend too much time on the consumers once they have been captured.

7.1.3   Increasing m_P

According to Theorem 4.5, if

$$m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}, \ \ 1 + \frac{1}{2}e_Ch_CK_C > \frac{1 + e_{CP}h_{CP}K_C}{e_Ph_P}$$

then increasing m_P makes it harder for the resource to invade.

Biological Remark: To be in this case, the predators must have a sufficiently small natural mortality rate and must gain sufficiently from consuming the consumers. In addition, they must spend a sufficiently small amount of time handling the consumers. So, there is not much to limit the growth of the predators. Increasing m_P means less predators to feed upon the resource, which helps the resource. It also means fewer predators to feed upon the consumers, but in order to be in this case, the consumers must have a sufficiently large amount of intraspecific interference, so more consumers means more intraspecific interference, which also helps the resource.

If

$$m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}, \quad 1+\frac{1}{2}e_Ch_CK_C < \frac{1+e_{CP}h_{CP}K_C}{e_Ph_P}, \quad e_{RC} >> e_{RP}$$

then increasing m_P makes it harder for the resource to invade.

Biological Remark: In this case, the primary source of predation on the resource comes from the consumers. Increasing m_P means less predators to suppress the consumers.

If

$$m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}, \quad 1+\frac{1}{2}e_Ch_CK_C < \frac{1+e_{CP}h_{CP}K_C}{e_Ph_P}, \quad e_{RC} << e_{RP}$$

then increasing m_P makes it easier for the resource to invade.

Biological Remark: In this case, the primary source of predation on the resource comes from the predators. Increasing m_P means less predators to consume the resource.

If

$$m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}, \quad e_{RC} >> e_{RP}$$

then increasing m_P makes it easier for the resource to be excluded.

Biological Remark: In this case, the primary source of predation on the resource comes from the consumers. Increasing m_P means less predators to suppress the consumers.

If

$$m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}, \quad e_{RC} << e_{RP}$$

then increasing m_P makes it harder for the resource to be excluded.

Biological Remark: In this case, the primary source of predation on the resource comes from the predators. Increasing m_P means less predators to consume the re-

source.

If

$$m_P > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$$

then increasing m_P makes it easier for the resource to invade and harder for them to be excluded.

Biological Remark: Here, $\alpha_{CP}e_{CP}$ is small so the predators do not gain much from consuming the consumers, so the predators need have greater need for the resource. Increasing m_P means there are fewer predators to consume the resource.

7.1.4   Increasing $e_P h_P$

According to Theorem 4.6, if

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) > 0, \ e_{RC} >> e_{RP}$$

then increasing $e_P h_P$ makes invasion harder. If

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) > 0, \ e_{RC} << e_{RP}$$

then increasing $e_P h_P$ makes invasion easier. If

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) > 0, \ e_{RC} >> e_{RP}$$

then increasing $e_P h_P$ makes exclusion easier. If

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) > 0, \ e_{RC} << e_{RP}$$

then increasing $e_P h_P$ makes exclusion harder. If

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) < 0$$

then increasing $e_P h_P$ makes it harder for the resource to invade and easier for them to be excluded.

Biological Remark: In the case where the resource's primary threat from predation are the consumers, increasing $e_P h_P$ means the predators spend more time interfering with each other and less time hunting consumers, so there are more consumers to feed upon the resource, which is worse for the resource. In the case where the resource's primary threat from predation are the predators, increasing $e_P h_P$ means the predators spend more time interfering with each other and less time feeding upon the resource, which is good for the resource.

7.1.5   Increasing e_{CP}

According to Theorem 4.7, if

$$e_{CP} > \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \quad m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$$

then increasing e_{CP} makes it easier for the resource to invade.

Biological Remark: In this case, the predators are sufficiently efficient at gaining from feeding upon consumers compared to the time they spend handling encountered consumers. Thus, the predators gain more by increasing e_{CP} than they lose by the increased time they spend handling encountered consumers. In this case, e_{CP} is already sufficiently large so the consumer growth rate is already sufficiently low. By increasing e_{CP} even further, this pushes the consumer growth rate even lower, which means even less food for the predators. This could then depress the predators' growth rate. So, there would be fewer consumers and fewer predators to attack the invading

resource, which would make invasion easier.

If

$$e_{CP} > \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ e_{RC} >> e_{RP}$$

then increasing e_{CP} makes it easier for the resource to be excluded, but if

$$e_{CP} > \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ e_{RC} << e_{RP}$$

then increasing e_{CP} makes it harder for the resource to be excluded.

Biological Remark: In the case where $e_{RC} >> e_{RP}$, the result is somewhat unexpected. We discuss this result in more detail in section 7.9.

In the case where $e_{RC} << e_{RP}$, the predators attack the resource much more than the consumers attack the resource. Increasing e_{CP} means the predators will spend more time searching for consumers. This leaves them less time to search for the resource, which makes it harder for the resource to be excluded.

If

$$e_{CP} < \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$$

or

$$m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ e_{CP} > 0$$

then increasing e_{CP} makes it harder for the resource to invade and harder for them to be excluded.

Biological Remark: In the case where $e_{CP} < \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}},$ the predators are sufficiently efficient at gaining from consuming the consumers compared to the amount of time they spend handling encountered consumers. But e_{CP} is sufficiently low so the predators do not attack the consumers too frequently. Increasing e_{CP}, while keeping it sufficiently low, means the consumer growth rate will be relatively high, but there will also be significantly more predators to feed upon

the invading resource. This makes invasion harder. But if the resource is already established, then e_{CP} being sufficiently low means the consumers and predators have significant time to search for the resource. Increasing e_{CP} means the consumers and predators spend more time interacting with each other. This leaves less time for them to search for the resource, which makes it harder for the resource to be excluded.

In the case where $m_P > \frac{1}{2} \frac{\alpha_{CP}}{h_{CP}}$, $e_{CP} > 0$, the predators are sufficiently inefficient at gaining from consuming the consumers compared to the amount of time they spend handling encountered consumers. Since the resource is absent from the system and trying to invade, the predators do not have another food source, so their growth rate is low. Increasing e_{CP} hurts the predators' growth rate, but since it is already low, it does not have a significant effect on the predators. But the decrease in predators helps the consumers' growth rate. This means there are more consumers to search for the resource. This has a net negative effect on the resource's chances of invading. But when the resource is already established, the consumers have to spend more trying to avoid predators. This takes away from time they could otherwise spend searching for the resource. This makes exclusion harder.

7.1.6   Increasing h_{CP}

According to Theorem 4.8, if

$$h_{CP} < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C + m_P}{e_{CP}K_C m_P}$$

then increasing h_{CP} makes it harder for the resource to invade and harder for them to be excluded.

Biological Remark: In this case, the predators spend a small amount of time handling each captured consumer. Increasing h_{CP} means the predators spend more time on each consumer, which slows its growth rate. This helps the consumers,

which then makes it harder for the resource to invade. But if the resource is already established then the predators are already spending time feeding upon the resource, so increasing h_{CP} means the predators have to take some of the time they were spending on handling the resource to handle the consumers, which helps the resource.

If

$$h_{CP} > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C + m_P}{e_{CP}K_C m_P}$$

then increasing h_{CP} makes it easier for the resource to invade and keeps exclusion the same.

Biological Remark: In this case, the predators spend a large amount of time handling each captured consumer. Increasing h_{CP} does not decrease the growth rate of the predators much or increase the growth rate of the consumers much. But it does reduce the amount of time the predators have to consume the resource, which benefits the resource. But if the resource is already established, then the predator does not have much time to attack the resource and increasing h_{CP} does not change this.

7.1.7 Increasing h_{PC}

According to Theorem 4.9, if

$$\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$$

then increasing h_{PC} makes it easier for the resource to invade and harder for them to be excluded.

Biological Remark: In this case, the predators' mortality rate is sufficiently small compared to how efficiently they gain from consuming the consumers. Increasing h_{PC} means the consumers spend more time avoiding predators. This leaves them less time to search for the resource. In addition, the predators need to spend more

time searching for the consumers, which also leaves them less time to search for the resource.

If

$$\frac{1}{2}\alpha_{CP}e_{CP} - m_P(1 + e_{CP}h_{CP}K_C) < 0$$

then increasing h_{PC} keeps invasion and exclusion the same.

Biological Remark: In this case, the predator mortality rate is sufficiently large compared to how efficient they gain from consuming the consumers. Thus, the predators have a limited impact on the consumers. Increasing h_{PC} does not significantly change the dynamics of the consumer-predator interactions, so their respective growth rates are not significantly changed. This means the number of consumers and predators searching for the resource is not significantly changed.

7.1.8   Increasing α_{CP}

According to Theorem 4.10, if

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ 1 + \frac{1}{2}e_Ch_CK_C < \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_Ph_P}, \ e_{RC} >> e_{RP}$$

then increasing α_{CP} makes it harder for the resource to invade. If

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ 1 + \frac{1}{2}e_Ch_CK_C < \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_Ph_P}, \ e_{RC} << e_{RP}$$

then increasing α_{CP} makes it easier for the resource to invade.

Biological Remark: These cases present unexpected results, which we will discuss in section 7.9.

If

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ 1 + \frac{1}{2}e_Ch_CK_C > \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_Ph_P}$$

then increasing α_{CP} makes it easier for the resource to invade.

Biological Remark: In this case, there is not as much intraspecific interference among the consumers and predators as there is interspecific interference between them. Increasing α_{CP} increases the predators' growth rate, which means there will be more predators, which will increase the amount of interspecific interference between the consumers and predators, which benefits the resource.

If

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ e_{RC} >> e_{RP}$$

then increasing α_{CP} makes it harder for the resource to be excluded.

Biological Remark: In this case, the primary source of predation on the resource is from the consumers. Increasing α_{CP} increases the predators' growth rate which hurts the consumers, which then helps the resource.

If

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ e_{RC} << e_{RP}$$

then increasing α_{CP} makes it easier for the resource to be excluded.

Biological Remark: In this case, the primary source of predation on the resource is from the consumers. Increasing α_{CP} increases the predator's growth rate, which hurts the resource.

If

$$\alpha_{CP} < \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}$$

then increasing α_{CP} makes it harder for the resource to invade and harder for them to be excluded.

Biological Remark: Since α_{CP} is sufficiently small in this case, we can view this situation as interspecific killing. We will discuss this situation in section 7.9.

7.2 Biological Remarks on Invasibility and Exclusion when Consumers Absent

7.2.1 Increasing K_R

According to Theorem 4.11, if

$$K_R > \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_Pe_{RP}h_{RP}}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$$

then increasing K_R makes it easier for the consumers to invade.

Biological Remark: Increasing K_R provides more food for the predators, which could make it harder for the consumers to invade. But the predators' growth rate eventually saturates, and in this case, K_R is already sufficiently large. So, increasing K_R does not provide as much food for the predators as it does for the invading consumers.

If either

$$K_R < \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_Pe_{RP}h_{RP}}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ \alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$$

or

$$m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_R > 0, \ \alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$$

then increasing K_R makes it easier for the consumers to invade. But if either

$$K_R < \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_Pe_{RP}h_{RP}}, \ m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ \alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$$

or

$$m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \ K_R > 0, \ \alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$$

then increasing K_R makes it harder for the consumers to invade.

Biological Remark: Increasing K_R means more food for the predators and therefore more predators to consume the consumers. But it also means more food for the

consumers. In the case where $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$, the consumers gain much more than the predators do from consuming the resource. In this case, the increase in K_R benefits the consumers more than the predators, which makes it easier for the consumers to invade. But in the case where $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$, the predators gain much more than the consumers do from consuming the resource. In this case, increasing K_R benefits the predators more than the consumers, which means more predation on the consumers. This makes it harder for the consumer to invade.

If

$$K_R > \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_P e_{RP} h_{RP}}, \; m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \; e_{CP}h_{CP} > e_P h_P$$

then increasing K_R makes it easier for the consumers to be excluded.

Biological Remark: In this case, the predators spend sufficiently little time interfering with each other and they are sufficiently efficient in how much they gain by consuming the consumers compared to the time they spend interacting with encountered consumers. By increasing K_R, there is more food for the predators, which leads to more predators to consume the consumers. Since there is a sufficiently small amount of intraspecific interference among the predators and the predators' mortality rate is sufficiently low, this makes it easier for the consumers to be excluded.

If

$$K_R > \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_P e_{RP} h_{RP}}, \; m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \; e_{CP}h_{CP} < e_P h_P, \; e_{CP} >> e_{RC}$$

then increasing K_R makes it easier for the consumers to be excluded. But, if

$$K_R > \frac{m_P}{\frac{1}{2}\alpha_{RP}e_{RP} - m_P e_{RP} h_{RP}}, \; m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \; e_{CP}h_{CP} ><_P h_P, \; e_{CP} << e_{RC}$$

then increasing K_R makes it harder for the consumers to be excluded.

Biological Remark: Increasing K_R means there will be more predators to attack

the consumers but also more resource for the consumers to attack and feed upon. In the case where $e_{CP} >> e_{RC}$, the predators attack the consumers much more than the consumers attack the resource. In this case, increasing K_R increases the attack rate on the consumers by the predators more than it increases the attack rate by the consumers on the resource. This makes it easier for the consumers to be excluded. But in the case where $e_{CP} << e_{RC}$, the consumers attack the resource much more than the predators attack the consumers. In this case, increasing K_R increases the attack rate by the consumers on the resource more than it increases the attack rate on the consumers by the predators. This makes it harder for the consumers to be excluded.

7.2.2   Increasing α_{RP}

According to Theorem 4.12, if

$$\alpha_{RP} > \frac{2m_P(1 + h_{RP}e_{RP}K_R)}{e_{RP}K_R}, \ \alpha_{RP} >> \frac{\alpha_{RC}e_{RC}}{2e_{CP}}$$

then increasing α_{RP} makes it easier for the consumers to invade. But, if

$$\alpha_{RP} > \frac{2m_P(1 + h_{RP}e_{RP}K_R)}{e_{RP}K_R}, \ \alpha_{RP} << \frac{\alpha_{RC}e_{RC}}{2e_{CP}}$$

then increasing α_{RP} makes it harder for the consumers to invade.

Biological Remark: If $\alpha_{RP} >> \frac{\alpha_{RC}e_{RC}}{2e_{CP}}$ then the predator attack rate on the consumers is sufficiently high compared to what the consumers gain from consuming the resource. Increasing α_{RP} increases the predators' growth rate, which should hurt the consumers. This should make invasion harder rather than easier. One possible explanation for why this does not happen is that perhaps, in this case, the predators grow so fast that they overconsume the resource. This does not hurt the consumers too much since they were not gaining much from the resource in the first place, but

it causes the predators' growth rate to decrease. This helps the consumers invade. If $\alpha_{RP} << \frac{\alpha_{RC}e_{RC}}{2e_{CP}}$ then the predator attack rate on the consumers is sufficiently low compared to what the consumers gain from consuming the resource. Increasing α_{RP} increases the predator's growth rate, which means there are more predators to compete with for the resource. This hurts the consumers. Also, since the predator attack rate on the consumers is sufficiently low, having more predators means the consumers have to spend more time avoiding predators in order to enjoy the same survival comfort that comes with a low attack rate.

If

$$\alpha_{RP} > \frac{2m_P(1 + h_{RP}e_{RP}K_R)}{e_{RP}K_R}$$

then increasing α_{RP} makes it easier for the consumers to be excluded.

Biological Remark: If the consumers are already established, then increasing α_{RP} will increase the predators' growth rate, which will lead to more predators to feed upon the consumers.

If

$$\alpha_{RP} < \frac{2m_P(1 + h_{RP}e_{RP}K_R)}{e_{RP}K_R}$$

then increasing α_{RP} makes it harder for the consumers to invade.

Biological Remark: Increasing α_{RP} will increase the predators' growth rate, which will lead to more predators to feed upon the consumers.

7.2.3   Increasing m_P

According to Theorem 4.13, if

$$m_P < \frac{\alpha_{RP}e_{RP}K_R}{2(1 + h_{RP}e_{RP}K_R)}, \quad 2e_{CP}\alpha_{RP} << \frac{1}{2}\alpha_{RC}e_{RC}$$

then increasing m_P makes it easier for the consumers to invade.

Biological Remark: In this case, the predators gain sufficiently little from consuming the resource and the consumers' growth rate due to consuming the resource is much greater than the rate at which consumers are attacked by predators. So, increasing m_P means less predators to consume the consumers, which helps the consumers invade.

If

$$m_P < \frac{\alpha_{RP} e_{RP} K_R}{2(1 + h_{RP} e_{RP} K_R)}, \ 2e_{CP}\alpha_{RP} >> \frac{1}{2}\alpha_{RC} e_{RC}$$

then increasing m_P makes it harder for the consumers to invade.

Biological Remark: This situation presents an unexpected result, which we will discuss in more detail in section 7.9.

If

$$m_P < \frac{\alpha_{RP} e_{RP} K_R}{2(1 + h_{RP} e_{RP} K_R)}$$

then increasing m_P makes it harder for the consumers to be excluded.

Biological Remark: Increasing m_P means there are fewer predators to feed upon the consumers.

If

$$m_P > \frac{\alpha_{RP} e_{RP} K_R}{2(1 + h_{RP} e_{RP} K_R)}$$

then increasing m_P makes it easier for the consumers to invade.

Biological Remark: Increasing m_P means there are fewer predators to feed upon the consumers.

7.2.4 Increasing $e_P h_P$

According to Theorem 4.14, increasing $e_P h_P$ makes it easier for the consumers to invade, and if

$$\frac{1}{2}\alpha_{RP} e_{RP} K_R - m_P(1 + h_{RP} e_{RP} K_R) > 0$$

then increasing $e_P h_P$ makes it harder for the consumers to be excluded.

Biological Remark: Increasing $e_P h_P$ means the predators interfere with each other more, which means they spend less time hunting consumers.

7.2.5 Increasing h_{RP}

According to Theorem 4.15, if

$$h_{RP} < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P}{m_P e_{RP}K_R} \Rightarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R > m_P$$

then increasing h_{RP} makes it harder for the consumers to invade and harder for the consumers to be excluded.

Biological Remark: In this case, the predators spend a sufficiently small amount of time handling the resource compared to what they gain from consuming the resource. Increasing h_{RP} means the predators take more time to handle encountered resource, which increases the amount of resource. But, if h_{RP} remains sufficiently small compared to what the predators gain from consuming the resource, then the increase in resource is more beneficial to the predators than the increase in h_{RP} is detrimental, so increasing h_{RP} increases the predator population, which hurts the invading consumers. But, if the consumers are already established then the increase in resource is enough to overcome the increase in predators, so increasing h_{RP} helps already present consumers.

If

$$h_{RP} > \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R - m_P}{m_P e_{RP}K_R} \Leftarrow \frac{1}{2}\alpha_{RP}e_{RP}K_R < m_P$$

then increasing h_{RP} makes it easier for the consumers to invade.

Biological Remark: Increasing h_{RP} means the predators spend more time handling the resource, which means they have less time available to spend attacking the consumers.

7.2.6 Increasing e_{RP}

According to Theorem 4.16, increasing e_{RP} makes it harder for the consumers to invade, and if

$$e_{RP} > \frac{m_P}{\frac{1}{2}\alpha_{RP} - m_P h_{RP} K_R}, \quad m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$$

then increasing e_{RP} makes it easier for the consumers to be excluded.

Biological Remark: Increasing e_{RP} increases the predators' growth rate and decreases the amount of resource available to the consumers to feed on. Both of these hurt the consumers.

7.3 Biological Remarks on Invasibility and Exclusion when Predators Absent and $0 < R^* < K_R$

7.3.1 Increasing K_C

According to Theorem (4.17), if $0 < R^* < K_R$ then increasing K_C always makes it easier for the predator to invade.

Biological Remark: Increasing K_C increases the amount of food available for the predators to consume, which makes is easier for the predators to invade.

If $0 < R^* < K_R$, $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C \Leftrightarrow K_C > \frac{e_{RC} h_{RC} K_R - 1}{e_C h_C}$, $e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$, and $K_C > K_C^*$, where K_C^* is a solution to equation (4.60), then increasing K_C makes it easier for the predators to invade.

Biological Remark: One way to have $e_C h_C < \frac{e_{CP} h_{CP} \alpha_{RC} e_{RC} K_R}{r_C}$ is if $e_{CP} h_{CP}$ is sufficiently large. But this would mean that the predators spend a sufficiently large amount of time handling the consumers. If $K_C > K_C^*$ then increasing K_C means there are more consumers for the predators to attack and handle, which reduces the predators' growth rate. Additionally, more consumers reduces the resource's growth rate which leads to a further reduction in the predators' growth rate.

If $0 < R^* < K_R$, $e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C \Leftrightarrow K_C > \frac{e_{RC}h_{RC}K_R-1}{e_Ch_C}$, and $0 < K_C < K_C^*$ then increasing K_C makes it easier for the predators to be excluded when $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ and harder when $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$.

Biological Remark: Increasing K_C means there are more consumers for the predators to feed upon, and more consumers to feed upon the resource. If $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then the predators gain more from consuming the resource than the consumers. In this case, the increase in the number of consumers hurts the predators, which makes exclusion easier. But if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then the predators gain more from consuming the consumers than the resource. In this case, the increase in the number of consumers helps the predators, which makes exclusion harder.

If $0 < R^* < K_R$, $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R \Leftrightarrow K_C < \frac{e_{RC}h_{RC}K_R-1}{e_Ch_C}$, and $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then increasing K_C makes it easier for the predators to be excluded. But if $1 + e_Ch_CK_C < e_{RC}h_{RC}K_R$ and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then increasing K_C makes it harder for the predators to be excluded.

Biological Remark: Increasing K_C means there are more consumers to consume the resource. Since both species are food sources for the predators, the effect could potentially help or hurt the predators. In the case where $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$, the the predators gain more from consuming the resource than consuming the consumers. In this case, the decrease in the resource hurts the predators more than the increase in consumers. But in the case where $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$, the predators gain more from consuming the resource than consuming the consumers. In this case, the increase in consumers helps the predators more than the decrease in the resource hurts the predators.

7.3.2 Increasing K_R

According to Theorem 4.18, if $0 < R^* < K_R$ then increasing K_R makes it harder for the predators to invade and harder for them to be excluded.

Biological Remark: This situation presents an unexpected result, which we will discuss in section 7.9.

7.3.3   Increasing α_{RC}

According to Theorem 4.19, if $0 < R^* < K_R$ then increasing α_{RC} makes it harder for the predators to invade and easier for the predators to be excluded.

Biological Remark: Increasing α_{RC} means the consumers are more efficient in gaining from consuming the resource. This allows the consumers to grow faster, which can reduce the resource population. This in turn can reduce the consumer population. Both of these mean the predators end up with less food.

7.3.4   Increasing e_{RC}

According to Theorem 4.20, if $0 < R^* < K_R$ then increasing e_{RC} makes it harder for the predators to invade and harder for the predators to be excluded.

Biological Remark: Increasing e_{RC} means the consumers encounter the resource more frequently. This increases the consumers' growth rate but also increases the amount of time they spend handling the resource. When the predators are invading, their population density is low so consumers can afford the extra handling time required to reduce the resource population. But the reduction in resource population reduces the predator population so there is less food for the invading predators.

But when the predators are established, the consumers need to worry about avoiding predation so they cannot spend all of their time encountering and handling the resource. So the limited amount of extra consumption on the resource has a net positive effect on the consumers' growth rate. This means more food for the predators.

7.3.5 Increasing $e_C h_C$

According to Theorem 4.21, if $0 < R^* < K_R$ and $e_{RC} h_{RC} K_R < 1 + e_C h_C K_C \Leftrightarrow e_C h_C > \frac{e_{RC} h_{RC} K_R - 1}{K_C}$ then increasing $e_C h_C$ makes it easier for the predators to invade and easier for the predators to be excluded.

Biological Remark: Increasing $e_C h_C$ means the consumers spend more time interfering with each other. If the predators are trying to invade, then this means there will be less competition for the resource, which helps the predators. But if the predators are established, they need a sufficient amount of food to avoid being excluded from the system and more intraspecific interference among the consumers inhibits the growth rate of the consumers, which reduces the amount of food they provide to the predators.

If $0 < R^* < K_R$ and $1 + e_C h_C K_C < e_{RC} h_{RC} K_R \Leftrightarrow e_C h_C < \frac{e_{RC} h_{RC} K_R - 1}{K_C}$ then increasing $e_C h_C$ has no effect on whether the predators can invade or are excluded from the system.

Biological Remark: In this case, $e_C h_C$ is sufficiently small, so as long as $e_C h_C$ remains sufficiently small after it increased, there is no significant reduction in the consumers' growth rate and no significant increase in the resource's growth rate as a result of this increased intraspecific interference.

7.3.6 Increasing r_C

According to Theorem 4.22, if $0 < R^* < K_R$ then increasing r_C makes it easier for the predators to invade and easier for them to be excluded from the system.

Biological Remark: Increasing r_C increases the growth rate of the consumers, which means more food for the invading predators. But if the predators are established in the system, then increasing r_C and increasing the growth rate on the consumers means more consumers to consume the resource, which reduces the amount of resource available to both the consumers and predators, and reduced resource for the

consumers reduces the amount of consumers available for the predators to consume.

7.3.7 Increasing h_{RC}

According to Theorem 4.23, if $0 < R^* < K_R$ and $e_{RC}h_{RC}K_R < 1 + e_C h_C K_C \Leftrightarrow h_{RC} < \frac{1 + e_C h_C K_C}{e_{RC}K_R}$ then increasing h_{RC} makes it easier for the predators to invade and easier for the predators to be excluded.

Biological Remark: Increasing h_{RC} increases the amount of time consumers spend handling encountered resource. When the predators are trying to invade, the extra time consumers spend handling encountered resource reduces the amount of competition, which helps the predators invade. But when the consumers are established, the increased handling time consumers spend handling encountered resource reduces the consumers' growth rate, which means less food for the predators.

If $0 < R^* < K_R$ and $1 + e_C h_C K_C < e_{RC}h_{RC}K_R \Leftrightarrow h_{RC} > \frac{1 + e_C h_C K_C}{e_{RC}K_R}$ then increasing h_{RC} has no effect on whether the predators can invade or are excluded from the system.

Biological Remark: In this case, the consumers already spend a sufficiently large amount of time handling the encountered resource that the consumer growth rate is sufficient low that more time spent handling encountered resource will not effect its growth rate enough to change whether the predators can invade or are excluded.

7.4 Biological Remarks on Invasibility and Exclusion when Predators Absent and $\frac{K_R}{2} < R^* < K_R$

7.4.1 Increasing K_C

According to Theorem 4.24, if $\frac{K_R}{2} < R^* < K_R$ and $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then increasing K_C makes it easier for the predators to invade and harder for the predators to be

excluded.

Biological Remark: In this case, the predators gain more from consuming the consumers than consuming the resource so increasing K_C means more consumers for the predators to consume, which benefits the predators.

If $\frac{K_R}{2} < R^* < K_R$ and $\alpha_{RP} e_{RP} K_R >> \alpha_{CP} e_{CP} K_C$ then increasing K_C makes it harder for the predators to invade and easier for the predators to be excluded.

Biological Remark: In this case, the predators gain more from consuming the resource than consuming the consumers. Increasing K_C means there are more consumers to feed upon the resource. The negative effect of less resource outweighs the positive effect of more consumers to feed upon, so increasing K_C has a net negative effect on the predators.

7.4.2   Increasing K_R

According to Theorem 4.25, if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then increasing K_R makes it harder for the predators to invade. But if $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then increasing K_R makes it easier for the predators to invade.

Biological Remark: If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then the predators gain more from consuming the resource than consuming the predators. Increasing K_R means more resource for the predators to consume, which helps them to invade. If $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then the predators gain more from consuming the consumers than consuming the resource. Increasing K_R means more resource for the consumers to consume, which should increase the consumers' growth rate. This, in turn, should mean more consumers for the predators to feed upon, which should be beneficial for the predators. However, this does not appear to be the case. One possible explanation for why increasing K_R might be more harmful than helpful to the predators in this case is that the increase in the consumer population might not lead to a significant increase in the predator population. However, increasing K_R means more resource for the

predators to encounter. The more time the predators spend attacking the resource, the less time they have for attacking the consumers. And since the predators gain more from consuming the consumers than the resource in this case, the decrease in attacks on the consumers harms the predators' ability to invade.

If $\frac{K_R}{2} < R^* < K_R$, $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_C h_C K_C \Leftrightarrow K_R < \frac{1+e_C h_C K_C}{\frac{1}{2}e_{RC}h_{RC}}$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) > \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$ and $0 < K_R < K_R^*$, where K_R^* is the positive root of equation (4.74) then increasing K_R makes it harder for the predators to be excluded. If $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2}e_{RC}h_{RC}K_R > 1 + e_C h_C K_C \Leftrightarrow K_R > \frac{1+e_C h_C K_C}{\frac{1}{2}e_{RC}h_{RC}}$ then increasing K_R also makes it harder for the predaators to be excluded. In all other cases, if $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ then increasing K_R makes it easier for the predators to be excluded. But if $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ then increasing K_R makes it harder for the predators to be excluded.

Biological Remark: In the cases where $\alpha_{RP}e_{RP} << \alpha_{CP}e_{CP}$ or $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$, the reasoning follows the same as above for invasion. When $K_R < \frac{1+e_C h_C K_C}{\frac{1}{2}e_{RC}h_{RC}}$, $\alpha_{RC}e_{RC}(1 + e_{CP}h_{CP}K_C) > \frac{1}{2}r_C e_{RP}h_{RP}(1 + e_C h_C K_C)$ and $0 < K_R < K_R^*$ then the resource population is sufficiently small, but the consumers gain sufficiently from consuming the resource, the predators spend a sufficiently small amount of time handling the resource, and/or lots of time handling consumers. Increasing K_R means there is more resource which increases the number of consumers. This, in turn, increases the amount of time the predators spend handling consumers. This hurts the predators and makes exclusion easier. And when $K_R > \frac{1+e_C h_C K_C}{\frac{1}{2}e_{RC}h_{RC}}$, there is a sufficiently large amount of resource already available to the predators. But the consumers spend a sufficiently large amount of time handling the resource. So increasing K_R means more resource for the consumers to handle, which hurts their growth rate. A reduction in the growth rate of the consumers hurts the predators, which makes exclusion easier.

7.4.3 Increasing α_{RC}

According to Theorem 4.26, if $\frac{K_R}{2} < R^* < K_R$ then increasing α_{RC} makes it harder for the predators to invade and harder for the predators to be excluded.

Biological Remark: Increasing α_{RC} means the consumers gain more from consuming the resource, which increases the consumers' growth rate. When the predators are absent from the system and trying to invade, the increase in the consumers' growth rate reduces the amount of the resource, which in turn can reduce the amount of consumers, which would have a negative effect on the predators. But if the predators are established in the system, the increase in the consumer growth rate means more food for the predators. The increase in the predator population helps control the consumer population so the consumers cannot reduce the resource population too significantly.

7.4.4 Increasing e_{RC}

According to Theorem 4.27, if $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2}e_{RC}h_{RC}K_R < 1 + e_Ch_CK_C \Leftrightarrow e_{RC} < \frac{1+e_Ch_CK_C}{\frac{1}{2}h_{RC}K_R}$ then increasing e_{RC} makes it harder for the predators to invade and harder for the predators to be excluded.

Biological Remark: Increasing e_{RC} means the consumers encounter the resource more often. To be in this case, the encounter must be sufficiently small and the intraspecific interference must be sufficiently high. When the predators are absent, this increased encounter rate leads to less resource for the predators to feed upon. Also, more encounters should increase the consumer growth rate, but more consumers leads to more intraspecific interference, which limits the consumer growth rate. On the other hand, when the predators are already present in the system, their presence keeps the consumer population from growing too much as a result of the increased encounter rate that they severely deplete the amount of resource or see their own population grow enough that intraspecific interference becomes a more significant

factor.

If $\frac{K_R}{2} < R^* < K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R \Leftrightarrow e_{RC} > \frac{1 + e_C h_C K_C}{\frac{1}{2} h_{RC} K_R}$ then increasing e_{RC} has no effect on whether the predators can invade or are excluded from the system.

Biological Remark: To be in this case, e_{RC} must be sufficiently large and K_C must be sufficiently small. Since K_C is sufficiently small, the consumers can only deplete the resource so much and since e_{RC} is already sufficiently large, the consumers are already encountering the resource almost as much as possible. So increasing e_{RC} does not significantly change the consumers' growth rate, which in turn does not significantly change the resource's population density.

7.4.5 Increasing h_{RC}

According to Theorem 4.28, if $\frac{K_R}{2} < R^* < K_R$ then increasing h_{RC} makes it easier for the predators to invade and easier for the predators to be excluded.

Biological Remark: Increasing h_{RC} increases the amount of time consumers spend handling encountered resource. When the predators are absent, increasing the handling time decreases the consumer growth rate, which in turn increases the resource population, meaning more food for both the predators and consumers. But more food for the consumers increases the consumer population, which means more food for the predators. But when the predators are present, increasing the handling time decreases the consumer population's growth rate. This means less food for the predators.

7.4.6 Increasing $e_C h_C$

According to Theorem 4.29, if $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C \Leftrightarrow e_C h_C > \frac{\frac{1}{2} e_{RC} h_{RC} K_R - 1}{K_C}$ then increasing $e_C h_C$ makes it easier for the predators to invade and easier for the predators to be excluded.

Biological Remark: To be in this case, $e_C h_C$ must already be sufficiently large.

Increasing $e_C h_C$ increases the amount of intraspecific interference among the consumers, which reduces the consumers' growth rate, although not significantly since $e_C h_C$ was already sufficiently large. But the reduction in the consumers' growth rate leads to an increase in the amount of resource, which leads to more food for both the consumers are resource. The increase in food for the consumers leads to more consumers, which also means more food for the predators.

If $\frac{K_R}{2} < R^* < K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R \Leftrightarrow e_C h_C < \frac{\frac{1}{2} e_{RC} h_{RC} K_R - 1}{K_C}$ then increasing $e_C h_C$ does not effect whether the predators can invade or are excluded from the system.

Biological Remark: To be in this case, $e_C h_C$ must be sufficiently small. We also must have K_C sufficiently small. Increasing $e_C h_C$ decreases the consumers' growth rate, but since K_C is sufficiently small, there are sufficiently few consumers to feed upon the resource so decreasing the consumers' growth rate does not significantly increase the amount of resource. Also, since K_C is sufficiently small, there are sufficiently few consumers for the predators to feed upon so decreasing the consumers' growth rate does not significantly decrease the amount of food available to the predators.

7.4.7 Increasing r_C

According to Theorem 4.30, if $\frac{K_R}{2} < R^* < K_R$ then increasing r_C makes it easier for the predators to invade.

Biological Remark: Increasing r_C increases the natural growth rate of the consumers, which increases the amount of food available to the predators.

If $\frac{K_R}{2} < R^* < K_R$ and $\frac{1}{2} e_{RC} h_{RC} K_R < 1 + e_C h_C K_C$ then increasing r_C makes it harder for the predators to be excluded.

Biological Remark: To be in this case, the consumers' intraspecific interference must be sufficiently large. Increasing r_C increases the consumers' growth rate, which

means more consumers for the predators to eat. Because the intraspecific interference is sufficiently large, the increased amount of consumers does not result in a proportional amount of additional consumption of the resource by the consumers, so the reduction in the resource's growth rate as a result of more consumers is not as significant to the predators' food supply as the increase in the consumer population.

If $\frac{K_R}{2} < R^* < K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$ then increasing r_C makes it easier for the predators to be excluded.

Biological Remark: To be in this case, the consumers' intraspecific interference must be sufficiently low. Increasing r_C increases the consumers' growth rate. Since there is a sufficiently small amount of intraspecific interference among the consumers, the increase in the consumer population leads to increased predation on the resource, which means less resource for both the consumers and predators to feed upon. The reduced amount of resource for the consumers to feed upon reduces the consumers' growth rate, which means less consumers for the predators to feed upon.

7.5   Harvesting

7.5.1   Harvesting only the Consumers in the $C - P$ Plane

In the unharvested case, $(0,0)$ is a saddle. The equilibrium point $(K_C, 0)$ is an unstable node provided that $e_{CP} K_C \alpha_{CP} > m_P (e_{RC} K_C h_{CP} + 1)$ and is a stable node if $e_{CP} K_C \alpha_{CP} < m_P (e_{RC} K_C h_{CP} + 1)$. In the case where $(K_C, 0)$ is an unstable node, the interior equilibrium point (C^*, P^*) exists and the system is permanent. But in the harvested case, $(0,0)$ is a saddle provided that $H_C < r_C$ but is a stable node if $H_C > r_C$. When $H_C > r_C$, the equilibrium point $\left(\left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$ is not biologically relevant.

Biological Remark: If H_C is sufficiently large, then both species will be driven to extinction. In order for the consumers to survive, we must have $H_C < r_C$.

7.5.2 Harvesting the Resource in the Full Model

According to Theorem 5.10, if $m_P > \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ then increasing H_R makes it easier for the consumers to be excluded if $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$ and harder to be excluded if $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$.

Biological Remark: In this case, the predators' mortality rate is large relative to the efficiency with which they are able to convert the resource into new predators. So, the predators do not gain much compared to the time they spend handling the resource. If $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$, the consumers gain much more from feeding upon the resource than the predators do. Because the predators do not gain much from consuming the resource, they need a large quantity of resource to sustain themselves. Harvesting the resource will therefore have a more significant affect on the predator population than on the consumer population. This will reduce the predator population which, in turn, puts less predation pressure on the consumers. This makes it easier for the consumers to invade. If $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$, then the consumers gain much less from feeding upon the resource than the predators do. Because of this, the predators do not feel the loss of the resource as much as the consumers do. Additionally, because predators are not efficient at handling the resource, a reduction in the amount of resource can benefit the predator population. This puts more predation pressure on the consumers, which makes invasion harder.

If $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ and $H_R > r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right]$ then increasing H_R makes it easier for the consumers to invade if $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$ and harder for the consumers to invade if $\alpha_{RP}e_{RP} >> \alpha_{RC}e_{RC}$. If $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$ and $H_R < r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right]$ then increasing H_R makes it harder for the consumers to invade.

Biological Remark: In this case, the predators gain sufficiently from consuming the resource compared to the time they spend handling encountered resource. When there is a sufficiently large amount of harvesting on the resource and $\alpha_{RP}e_{RP} << \alpha_{RC}e_{RC}$ then the consumers gain much more from feeding upon the resource than

the predators do. Because the predators do not gain much from consuming the resource, they need a large quantity of resource to sustain themselves. Harvesting the resource will therefore have a more significant affect on the predator population than on the consumer population. This will reduce the predator population which, in turn, puts less predation pressure on the consumers. This makes it easier for the consumers to invade. If there is a sufficiently large amount of harvesting on the resource and $\alpha_{RP} e_{RP} >> \alpha_{RC} e_{RC}$ then the consumers gain much less from feeding upon the resource than the predators do. Because of this, the predators do not feel the loss of the resource as much as the consumers do. This puts more predation pressure on the consumers, which makes invasion harder. When there is a sufficiently small amount of harvesting on the resource, then the predators population is relatively close to its equilibrium value in the non-harvested case. But, there is less resource for the consumers to feed upon when trying to invade. So harvesting has a greater effect on the consumer population in this case, which makes invasion harder.

If $m_P > \frac{1}{2} \frac{\alpha_{RP}}{h_{RP}}$ then increasing H_R makes it easier for the consumers to be excluded. If $m_P < \frac{1}{2} \frac{\alpha_{RP}}{h_{RP}}$ and $H_R > r_R \left[1 - \frac{m_P}{e_{RP} K_R \left(\frac{1}{2} \alpha_{RP} - m_P h_{RP} \right)} \right]$ then increasing H_R makes exclusion easier.

Biological Remark: When $m_P > \frac{1}{2} \frac{\alpha_{RP}}{h_{RP}}$, the predators do not gain sufficiently from consuming the resource compared to the time it takes them to handle encountered resource. Increasing H_R reduces the amount of resource, which reduces the amount of time the predators spend attacking the resource and increases the amount of time they can spend attacking the consumers. In the case where $m_P < \frac{1}{2} \frac{\alpha_{RP}}{h_{RP}}$ but $H_R > r_R \left[1 - \frac{m_P}{e_{RP} K_R \left(\frac{1}{2} \alpha_{RP} - m_P h_{RP} \right)} \right]$, the predators are sufficiently efficient at gaining from consuming the resource but there is already a sufficiently large amount of harvesting on the resource. Because of the large amount of harvesting already in the system, the predator population relies significantly on consuming the consumers so increasing H_R will increase the predators' dependence on the consumers. This will make it easier

for the consumers to be excluded.

If $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$, $H_R < r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right]$, and $e_{CP}h_{CP} > e_Ph_P$ then increasing H_R makes exclusion harder. If $m_P < \frac{1}{2}\frac{\alpha_{RP}}{h_{RP}}$, $H_R < r_R\left[1 - \frac{m_P}{e_{RP}K_R\left(\frac{1}{2}\alpha_{RP}-m_Ph_{RP}\right)}\right]$, and $e_{CP}h_{CP} < e_Ph_P$ then increasing H_R makes exclusion easier if $e_{CP} << e_{RC}$ and harder if $e_{CP} >> e_{RC}$.

Biological Remark: In this case, the predators are sufficiently efficient at gaining from consuming the resource compared to the time they spend handling the resource. Additionally, there is a sufficiently low amount of harvesting in the system. When $e_{CP}h_{CP} > e_Ph_P$, the predators spend a sufficiently small amount of time interfering with each other. So in this case, the main factor which limits the predator population is the time they spend handling consumers. Increasing H_R reduces the amount of resource for the predators to feed upon, making the predators more dependent on the consumers. But this means the predators will waste more time which will reduce their growth rate. This makes it harder for the consumers to be excluded. When $e_{CP}h_{CP} < e_Ph_P$, the predators spend a sufficiently large amount of time interfering with each other. If $e_{CP} << e_{RC}$ then the consumers attack the resource much more than the predators attack the consumers. Increasing H_R reduces the amount of resource the consumers can attack. This makes it easier for the consumers to be excluded. If $e_{CP} >> e_{RC}$ then the predators attack the consumers much more than the consumers attack the resource. Increasing H_R reduces the amount of resource for the predators to feed upon. This reduces the amount of predators who can attack the consumers, which makes it harder for the consumers to be excluded.

According to Theorem 5.11, if $0 < R^* < \left(\frac{r_R-H_R}{r_R}\right)K_R$, then increasing H_R makes it easier for the predators to invade and easier for the predators to be excluded.

Biological Remark: In this case, increasing H_R can drive the resource population closer to extinction. This means less food for the predators and consumers. Additionally, less food for the consumers reduces the consumer population, which reduces the

amount of food the consumers are able to provide for the predators. This seems that it should make invasion harder and exclusion easier. It is unclear what the mechanism is in this case which makes invasion easier.

According to Theorem 5.12, if $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R \Leftrightarrow H_R < r_R\left(1 - \frac{2(1 + e_C h_C K_C)}{e_{RC} h_{RC} K_R}\right) \Rightarrow 1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC} K_R$ and $\frac{1}{2} e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R < 1 + e_C h_C K_C$, and $\alpha_{RP} e_{RP} K_R \gg \alpha_{CP} e_{CP} K_C$ then increase H_R makes exclusion easier.

Biological Remark: In this case, the predators gain much more from consuming the resource than from consuming the consumers. Increasing H_R reduces the amount of resource available to the predators, which makes exclusion easier.

According to Theorem 5.13, if $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R \Leftrightarrow H_R > r_R\left(1 - \frac{2(1 + e_C h_C K_C)}{e_{RC} h_{RC} K_R}\right) \Leftarrow 1 + e_C h_C K_C > \frac{1}{2} e_{RC} h_{RC} K_R$ and $\alpha_{RP} e_{RP} K_R \ll \alpha_{CP} e_{CP} K_C$ then increasing H_R makes invasion easier. If $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R$ and $\alpha_{RP} e_{RP} K_R \gg \alpha_{CP} e_{CP} K_C$ then increasing H_R makes invasion harder. If $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $1 + e_C h_C K_C < \frac{1}{2} e_{RC} h_{RC}\left(\frac{r_R - H_R}{r_R}\right) K_R$ then increasing H_R makes exclusion easier.

Biological Remark: If $\alpha_{RP} e_{RP} K_R \ll \alpha_{CP} e_{CP} K_C$ then the predators gain much more from consuming the consumers than from consuming the resource. It is unclear why increasing H_R makes it easier for the predators to invade, as this reduces the amount of food available for the consumers which then reduces the amount of food available for the predators. If $\alpha_{RP} e_{RP} K_R \gg \alpha_{CP} e_{CP} K_C$ then the predators gain much more from consuming the resource than from consuming the consumers. Increasing H_R reduces the amount of resource available for the predators to consume, which makes it harder for the predators to invade. In either case, if the predators are established in the system, increasing H_R reduces the amount of food available to both the predators and to the consumers. The reduction in the consumer population

leads to a further reduction in the amount of food available to predators. This makes it easier for the predators to be excluded.

7.5.3 Harvesting the Consumers in the Full Model

According to Theorem 5.14, if $H_C < r_C \left(1 - \frac{m_P}{e_{CP}K_C\left(\frac{1}{2}\alpha_{CP}-h_{CP}m_P\right)}\right)$ and $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ then increasing H_C makes it easier for the resource to invade if $e_{CP}h_{PC} < e_Ph_P$ and harder to invade if $e_{CP}h_{CP} > e_Ph_P$. If $m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ or if $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ and $H_C > r_C \left(1 - \frac{m_P}{e_{CP}K_C\left(\frac{1}{2}\alpha_{CP}-h_{CP}m_P\right)}\right)$ then increasing H_C makes it easier for the resource to invade. In all cases, increasing H_C makes exclusion harder.

Biological Remark: This situation presents an unexpected result, which we will discuss in section 7.9.

According to Theorems 5.15 and 5.16, along with the comments following each of these theorems, if $\frac{1}{2}K_R < R^* < K_R$ and $\alpha_{RP}e_{RP}K_R >> \alpha_{CP}e_{CP}K_C$ then increasing H_C makes it harder for the predators to be excluded from the system.

Biological Remark: In this case, the predators gain much more from consuming the resource than consuming the consumers. Increasing H_C reduces the number of consumers who can feed upon the resource. This leaves more resource for the predators to feed upon, which makes it harder for the predators to be excluded.

7.5.4 Harvesting the Predators in the Full Model

According to Theorem 5.17, if $\frac{1}{2}\alpha_{CP}e_{CP}K_C-(m_P+H_P)(1+e_{CP}h_{CP}K_C) < 0 \Leftrightarrow H_P > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} \Leftarrow m_P > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$ then increasing H_P makes it easier for the resource to invade. If $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0 \Leftrightarrow H_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C} \Rightarrow m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1+e_{CP}h_{CP}K_C}$ then increasing H_P makes it harder for the resource to invade.

Biological Remark: Increasing H_P reduces the number of predators who can feed upon the resource and on the consumers. This allows the consumer population to grow more. On the one hand, there are fewer predators to consumer the resource. But

on the other hand, there are more consumers to consume the resource. It is unclear why increasing H_P benefits the resource when H_P is sufficiently large but hurts the resource when H_P is sufficiently small.

If $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0$ then increasing H_P makes it easier for the resource to be excluded if $e_{RC} >> e_{RP}$ and harder for the resource to be excluded if $e_{RC} << e_{RP}$. If $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) < 0$ then increasing H_P makes it easier for the resource to be excluded.

Biological Remark: If H_P is sufficiently small and $e_{RC} >> e_{RP}$ then the consumers attack the resource much more than the predators do. Increasing H_P reduces the number of predators who can feed upon the consumers. This allows the consumer population to increase and attack the resource more. This makes exclusion easier. If H_P is sufficiently small and $e_{RC} << e_{RP}$ then the predators attack the resource much more than the consumers do. Increasing H_P reduces the number of predators who can attack the resource. This makes exclusion harder. If H_P is sufficiently large then there are sufficiently few predators so the predators cannot attack the resource as frequently as the consumers do. Increasing H_P reduces the number of predators who can feed upon the consumer population, which allows the consumer population to increase. This makes it easier for the resource to be excluded.

According to Theorem 5.18, if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) > 0 \Leftrightarrow H_P < \frac{\frac{1}{2}\alpha_{RP}e - RPK_R}{1 + e_{RP}h_{RP}K_R} - m_P \Rightarrow m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$ and $e_{CP}\alpha_{RP} << \alpha_{RC}e_{RC}$ then increasing H_P makes it easier for the consumers to invade. If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) > 0$ and $e_{CP}\alpha_{RP} >> \alpha_{RC}e_{RC}$ then increasing H_P makes it harder for the consumers to invade. If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) < 0 \Leftrightarrow H_P > \frac{\frac{1}{2}\alpha_{RP}e - RPK_R}{1 + e_{RP}h_{RP}K_R} - m_P \Leftarrow m_P > \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$ then increasing H_P makes it easier for the consumers to invade. If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) > 0$ then increasing H_P makes it harder for the consumers to be excluded. If $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) < 0$ then the consumers cannot be excluded.

Biological Remark: Increasing H_P reduces the number of predators who can consume the consumers. It seems that this should make it easier for the consumers to invade and harder for them to be excluded. This is the situation in all cases, except when H_P is sufficiently small and $e_{CP}\alpha_{RP} >> \alpha_{RC}e_{RC}$. This situation presents an unexpected result, which we will discuss in section 7.9.

7.6   Harvesting in a Linear Food Web

When harvesting the resource, the important case to consider here is when we are near $\left(R^*, C^*, 0\right)$. In particular, if $e_{RC}h_{RC}\left(\frac{r_R - H_R}{r_R}\right)K_R < 1 + e_C h_C K_C \Leftrightarrow H_R > r_R\left(1 - \frac{1 + e_C h_C K_C}{e_{RC}h_{RC}K_R}\right) \Leftarrow 1 + e_C h_C K_C > e_{RC}h_{RC}K_R$ then harvesting the resource makes it easier for the predators to invade and easier for them to be excluded.

Biological Remark: Increasing H_R reduces the consumers' growth rate. This results in less food available to the predators. This makes it easier for the predators to be excluded, but it is unclear why this makes it easier for the predators to invade.

When harvesting the consumers, increasing H_C makes it easier for the resource to invade when it is the only species absent. In this case, increasing H_C makes invasion easier and exclusion harder.

Biological Remark: Because the only source of predation on the resource is from the consumers, increasing H_C reduces the amount of consumers who can feed upon the resource. This makes it easier for the resource to invade and harder for them to be excluded.

When harvesting the predators, the important case to consider is when are are near $\left(0, C^*, P^*\right)$. In the case where $\frac{1}{2}\alpha_{CP}e_{CP}K_C - (m_P + H_P)(1 + e_{CP}h_{CP}K_C) > 0 \Leftrightarrow H_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C} - m_P \Rightarrow m_P < \frac{\frac{1}{2}\alpha_{CP}e_{CP}K_C}{1 + e_{CP}h_{CP}K_C}$, increasing H_P makes it easier for the resource to invade and easier for them to be excluded.

Biological Remark: Increasing H_P reduces the number of predators who can feed upon the consumers. This increases the number of consumers who can feed upon the

resource, which makes it harder for the resource to invade and easier for them to be excluded.

7.7 Harvesting in Apparent Competition

When the resource is harvested near $\left(R^*, 0, P^*\right)$, it is harder for the consumers to invade the system. In the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R\right) > 0 \Leftrightarrow H_R > r_R\left(1 - \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{m_Pe_{RP}h_{RP}K_R}\right) \Leftarrow m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R}$, harvesting the resource makes it harder for the consumers to be excluded while in the case where $\frac{1}{2}\alpha_{RP}e_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R - m_P\left(1 + e_{RP}h_{RP}\left(\frac{r_R - H_R}{r_R}\right)K_R\right) < 0 \Leftrightarrow H_R < r_R\left(1 - \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{m_Pe_{RP}h_{RP}K_R}\right) \Rightarrow m_P < \frac{\frac{1}{2}\alpha_{RP}e_{RP}K_R}{1 + e_{RP}h_{RP}K_R}$, harvesting the resource makes it easier for the consumers to be excluded from the system.

Biological Remark: By harvesting the resource, the predator must rely more heavily on the consumers to sustain themselves. Thus, increasing H_R makes it harder for the consumers to invade. When H_R is sufficiently large, the predators already rely heavily on the consumers to sustain themselves. By increasing H_R, the is less food for the predators, but there is not too much more that the predators can rely on the consumers. So the predator population decreases, which makes it harder for the consumers to be excluded. But when H_R is sufficiently small, the predators will turn to the consumers more when H_R is increased. This makes it easier for the consumers to be excluded.

When $0 < R^*, \left(\frac{r_R - H_R}{r_R}\right)K_R$, increasing H_R makes it easier for the predators to invade and easier for them to be excluded.

Biological Remark: Since the predators feed upon the resource, increasing H_R means there is less resource for the predators to consume. This makes it easier for the predators to be excluded, but it is not clear why this makes it easier for the predators to invade.

When $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$ and $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then increasing H_R makes it harder for the predators to invade and easier for them to be excluded. When $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then increasing H_R makes it easier for the predators to invade and harder for them to be excluded.

Biological Remark: When $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$, the predators gain much more from consuming the resource than from consuming the consumers. Increasing H_R means there is less of the resource for the predators to consume, which hurts the predator population. This makes it harder for the predators to invade and easier for them to be excluded. When $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$, the predators gain much more from consuming the consumers than from consuming the resource. Increasing H_R reduces the number of resource available to the predators, which allows them to focus more on the consumers who they gain more from. This helps the predator population and makes it easier for them to invade while making it harder for them to be excluded.

Near $\left(0, C^*, P^*\right)$, increasing H_C in the case where $\frac{1}{2}\alpha_{CP} e_{CP} \left(\frac{r_C - H_C}{r_C}\right) K_C - m_P \left(1 + e_{RC} h_{RC} \left(\frac{r_C - H_C}{r_C}\right) K_C\right) < 0$ makes it easier for the resource to invade and harder for them to be excluded.

Biological Remark: Increasing H_C decreases the amount of food available to the predators. This reduces the predators' growth rate, which means there are fewer predators to feed upon the resource. This makes it easier for the resource to invade and harder for the resource to be excluded.

Near $\left(R^*, C^*, 0\right)$, increasing H_C makes it harder for the predators to invade. If $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$ then increasing H_C makes it harder for the predators to be excluded, but if $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$ then increasing H_C makes it easier for the predators to be excluded.

Biological Remark: Increasing H_C means there are fewer consumers for the predators to feed upon, which makes it harder for the predators to invade. When $\alpha_{RP} e_{RP} >> \alpha_{CP} e_{CP}$, the predators gain much more from consuming the resource than from con-

suming the consumers. Since the predators do not gain much from consuming the consumers, increasing H_C allows the predators to focus more on attacking the resource. This helps the predators and makes it harder for the predators to be excluded. When $\alpha_{RP} e_{RP} << \alpha_{CP} e_{CP}$, the predators gain much more from consuming the consumers than from feeding upon the resource. Increasing H_C, reduces the number of consumers the predators can feed upon, which makes it easier for the predators to be excluded.

7.8 Harvesting in Resource Competition

When harvesting the resource, the important case to consider is the case when we are near $\left(R^*, C^*, 0\right)$. In the case where $0 < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$, the predators cannot invade the system and increasing H_R makes it easier for the predators to be excluded from the system. In the case where $\frac{1}{2}\left(\frac{r_R - H_R}{r_R}\right) K_R < R^* < \left(\frac{r_R - H_R}{r_R}\right) K_R$, increasing H_R makes it harder for the predators to invade the system and easier for them to be excluded from the system.

Biological Remark: Since the only food source for the predators in resource competition is the resource, increasing H_R reduces the amount of food available to the predators. This hurts the predators and makes it harder for them to invade while making it easier for them to be excluded.

When harvesting the consumers, we get that the invasibility and exclusion conditions near $\left(R^*, C^*, 0\right)$ are independent of H_C.

Biological Remark: Though the consumers and predators do not interact, the presence of the consumers affects the resource population level and so it seems that harvesting should have an indirect effect on the predator population's ability to invade or avoid exclusion. It is unclear why this indirect effect is not present.

7.9 Some Interesting Cases: A Closer Look

7.9.1 The Effect of Increasing e_{CP} on the Resource

According to Theorem 4.7, if

$$e_{CP} > \frac{m_P}{\frac{1}{2}\alpha_{CP}K_C - m_P h_{CP}K_C}, \;\; m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}, \;\; e_{RC} >> e_{RP}$$

then increasing e_{CP} makes it easier for the resource to be excluded.

Biological Remark: When $e_{RC} >> e_{RP}$, the consumers attack the resource much more than the predators attack the resource. Increasing e_{CP} increases the number of predators and decreases the number of consumers. At first glance, it seems that this should benefit the resource; making it harder for the resource to be excluded. Since e_{CP} is already sufficiently large, the consumer growth rate is already sufficiently depressed by the predators. Because the predators gain a sufficiently large amount from consuming the consumers compared to the amount of time they spend handling encountered consumers in this case, a further increase in e_{CP} significantly helps the predators. But this increase in predator growth rate results in a decrease in the consumer growth rate, which in turn decreases the predators' growth rate. If this decrease in the predators' growth rate is sufficiently large, the net effect on the consumers could be positive, which would make exclusion easier.

7.9.2 The Effect of Increasing α_{CP} on the Resource

According to Theorem 4.10, if

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \;\; 1 + \frac{1}{2}e_C h_C K_C < \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_P h_P}, \;\; e_{RC} >> e_{RP}$$

then increasing α_{CP} makes it harder for the resource to invade.

Biological Remark: In this case, the resource's main threat from predation is from

consumers. Increasing α_{CP} means the predators gain more from eating the consumers, which increases the predators' growth rate. This means there are more predators to feed upon the consumers, which reduces the number of consumers who can feed upon the resource. This seems like it should make invasion by the resource easier. One possible explanation why this does not happen is that perhaps, increased predation on the consumers due to a higher predator growth rate leads to a temporary reduction in the consumer population. This, in turn, leads to a reduction in the predator population, which ultimately allows for more consumers.

If

$$\alpha_{CP} > \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}, \ 1 + \frac{1}{2}e_Ch_CK_C < \frac{e_{CP}h_{PC}(1 + e_{CP}h_{CP}K_C)}{e_Ph_P}, \ e_{RC} << e_{RP}$$

then increasing α_{CP} makes it easier for the resource to invade.

Biological Remark: In this case, the resource's main threat from predation is from predators. Increasing α_{CP} means the predators gain more from eating the consumers, which increases the predators' growth rate. This means there are more predators to feed upon the resource. This seems like it should make invasion by the resource harder. One possible explanation why this does not happen is that perhaps, increased predation on the consumers due to a higher predator growth rate leads to a reduction in the consumer population. This ultimately leads to a reduction in the predator population.

If

$$\alpha_{CP} < \frac{2m_P(1 + e_{CP}h_{CP}K_C)}{e_{CP}K_C}$$

then increasing α_{CP} makes it harder for the resource to invade and harder for them to be excluded.

Biological Remark: Since α_{CP} is sufficiently small in this case, we can view this as being a situation as interspecific killing. In order for the predators to survive when

the resource is rare, m_P necessarily much be sufficiently small. Otherwise, the lack of resource combined with the predators' high mortality rate would lead to extinction of the predator. So, in this case, the predators need the resource. By increasing α_{CP} the predators's growth rate increases, but in order to remain in this case, α_{CP} cannot get too big, so the predators still cannot gain too much from feeding upon the consumers. Thus, the predators still need the resource. But, the increased predator growth rate leads to more predators to consume the resource which is bad for the resource. But if the resource is already established then the predators are already feeding upon the resource, so increasing α_{CP} increases the predators' growth rate which means they do not have as great a need for the resource.

7.9.3 The Effect of Increasing m_P on the Consumers

According to Theorem 4.13, if

$$m_P < \frac{\alpha_{RP} e_{RP} K_R}{2(1 + h_{RP} e_{RP} K_R)}, \ 2 e_{CP} \alpha_{RP} >> \frac{1}{2} \alpha_{RC} e_{RC}$$

then increasing m_P makes it harder for the consumers to invade.

Biological Remark: In this case, the predators attack the consumers at a sufficiently high rate, and the consumers do not gain much from consuming the resource compared to what the predators gain from consuming the resource. By increasing m_P, there should be fewer predators to consume the consumers, which should make invasion easier for the consumers. To see why this is not the case, let us consider the case with Holling II functional response. The system we have is

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RP} RP}{1 + e_{RP} h_{RP} R}$$
$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} RP}{1 + e_{RP} h_{RP} R} - m_P P$$
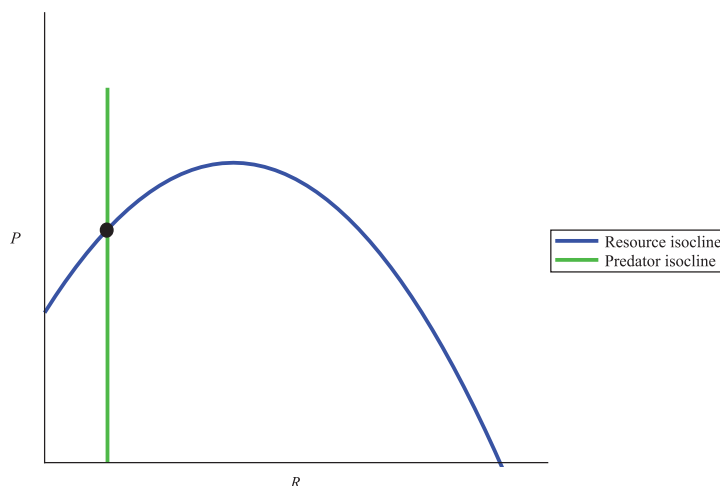
Figure 7.1: *Resource and predator isoclines in a predator-prey system with Holling II functional response.*

The predator isocline is the line $R^* = \frac{m_P}{e_{RP}(\alpha_{RP} - m_P h_{RP})}$. Thus, the resource and predator isoclines are as shown in Figure (7.1).

Notes:

1. $R^* \geq 0 \Leftrightarrow m_P < \frac{\alpha_{RP}}{h_{RP}}$

2. There is some critical value of R^* below which P^* is increasing and above which P^* is decreasing. But, $R^* = \frac{m_P}{e_{RP}(\alpha_{RP} - m_P h_{RP})}$ is an increasing function of m_P. Therefore, there is a critical value of m_P below which P^* is increasing and above which P^* is increasing.

3. The predation rate per predator, $\frac{e_{RP}}{1 + e_{RP} h_{RP} R^*}$ is a decreasing function of R^*.

So, increasing m_P increases R^*, which decreases the predation rate per predator. But this means that a fixed prey population can then support more predators, which increases the predator population provided m_P remains sufficiently small. Thus, when m_P is sufficiently small, increasing m_P has a greater positive effect on predator growth than negative effect from natural mortality. This benefit to the predator population hurts the consumer population so that increasing m_P makes it harder for the consumers to invade.
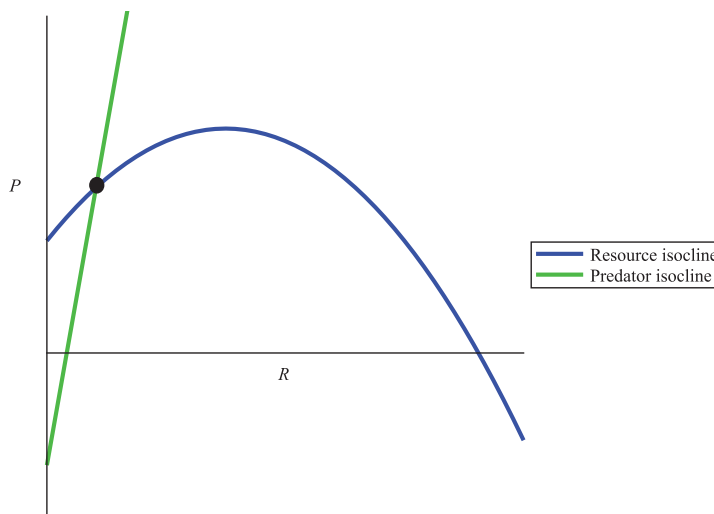
Figure 7.2: *Resource and predator isoclines in a predator-prey system with Beddington-DeAngelis functional response.*

In the case with Beddington-DeAngelis functional response, the system we have is

$$\frac{dR}{dt} = r_R R \left(1 - \frac{R}{K_R}\right) - \frac{e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P}$$
$$\frac{dP}{dt} = \frac{\alpha_{RP} e_{RP} R P}{1 + e_{RP} h_{RP} R + e_P h_P P} - m_P P$$

The predator isocline in this case is the line $P^* = \frac{e_{RP}(\alpha_{RP} - m_P h_{RP})}{e_P h_P} R^* - \frac{m_P}{e_P h_P}$. Thus, the resource and predator isoclines are as shown in Figure(7.2).

Just as in the case of Holling II functional response, there is some critical value of R^* below which P^* is increasing and above which P^* is decreasing. Note that the slope of the predator isocline is decreasing in $e_P h_P$ and the P-intercept of the predator isocline is increasing in $e_P h_P$. Thus, in order to be in the case where increasing R^* increases P^*, it is necessary to have $e_P h_P$ small. But if $e_P h_P$ is small, then the dynamics are approximately the same as in the Holling II case, which we discussed above. We can see that the slope of the predator isocline is decreasing in m_P, so assuming that $e_P h_P$ is small, then m_P sufficiently small and increasing implies that P^* is increasing.

Note: We know from [14] that $R^* = K_R$ is stable if $e_{RP} h_{RP} \left(1 - \frac{R^*}{K_R} \right) < 1$. So if $e_P h_P$ is not small, then P^* is near 0, so R^* is near K_R and so will not be in the case where increasing m_P increases P^*, even if m_P is small.

7.9.4 The Effect of Increasing K_R on the Predators

According to Theorem 4.18, if $0 < R^* < K_R$ then increasing K_R makes it harder for the predators to invade and harder for them to be excluded.

Biological Remark: Increasing K_R means there is more food for the consumers, which helps the consumer population to grow. When the predators are invading, the predator population is too low to significantly inhibit the growth of the consumers, so increasing the consumer population means more predation on the resource, which ends up decreasing both the resource and consumer population. This means there is less food for the invading predators. But, when the predator population is higher, the predator population can limit the growth of the consumer population, so that the consumers cannot depress the resource population too much. Thus, increasing K_R means both the resource and consumers will increase, which means more food for the predators, which helps keep it from being excluded.

7.9.5 The Effect of Harvesting the Consumer-Predator Subsystem

According to Theorem 5.1, if $H_C < r_C \left(1 - \frac{m_P}{K_C e_{CP} (\alpha_{CP} - h_{CP} m_P)} \right)$ then $\left(\left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$ is a saddle. But if $H_C > r_C \left(1 - \frac{m_P}{K_C e_{CP} (\alpha_{CP} - h_{CP} m_P)} \right)$ then $\left(\left(\frac{r_C - H_C}{r_C} \right) K_C, 0 \right)$ is a stable node.

Biological Remark: If $r_C \left(1 - \frac{m_P}{K_C e_{CP} (\alpha_{CP} - h_{CP} m_P)} \right) < H_C < r_C$ then the consumers can survive, while the predators go extinct. Thus, if the consumers are harvested at a sufficiently high rate, there will not be enough food to sustain the predator population.

7.9.6 The Effect of Harvesting Both Species in the Consumer-Predator Subsystem

According to Theorem 5.3, we will have coexistence in the consumer-predator subsystem with both species being harvested if we have that

$$
\begin{cases} H_P < \frac{\alpha_{CP}}{h_{CP}} - m_P \\ H_C < r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \right) \end{cases}
\Leftrightarrow
\begin{cases} H_P < \frac{\alpha_{CP}}{h_{CP}} \left(\frac{e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C}{\frac{1}{h_{CP}} + e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C} \right) - m_P \\ H_C < r_C \end{cases}
$$

But $r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \right) < r_C$ and $\frac{\alpha_{CP}}{h_{CP}} \left(\frac{e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C}{\frac{1}{h_{CP}} + e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C} \right) - m_P < \frac{\alpha_{CP}}{h_{CP}} - m_P$. So there is a tradeoff in the amount of harvesting that can be done on each species. If $H_C > r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \right)$ then the maximum value of H_P must be smaller than the case where $H_C < r_C \left(1 - \frac{m_P + H_P}{K_C e_{CP}[\alpha_{CP} - (m_P + H_P)h_{CP}]} \right)$. Similarly, if $H_P > \frac{\alpha_{CP}}{h_{CP}} \left(\frac{e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C}{\frac{1}{h_{CP}} + e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C} \right) - m_P$ then the maximum value of H_C must be smaller than the case where $H_P < \frac{\alpha_{CP}}{h_{CP}} \left(\frac{e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C}{\frac{1}{h_{CP}} + e_{CP}\left(\frac{r_C - H_C}{r_C} \right)K_C} \right) - m_P$. Biologically this is telling us that if we have a sufficiently large amount of harvesting on the consumers, then we must have less harvesting on the predators. Conversely, if we have a sufficiently large amount of harvesting on the predators, then we must have less harvesting on the consumers. The reason for this is that harvesting the consumers reduces the amount of food available to the predators. If the predators' food supply is shrinking because the consumers are being harvested more, then the predators cannot withstand being harvested as much. Similarly, if the predators are being harvested more, they need more food to help sustain themselves so the consumers cannot be harvested as much.

7.9.7 The Effect of Harvesting the Consumer in the Resource-Consumer Subsystem

According to Theorem 5.8, if $e_{RC} < r_R e_C h_C$ then the resource can always invade the system because the consumers either interfere with each other too much or do not encounter the resource enough to overcome the resource's intrinsic growth rate. When $e_{RC} > r_R e_C h_C$, the resource can invade provided that H_C is sufficiently large. Thus, harvesting the consumers can help facilitate invasion by the resource if harvesting has enough of an effect on the consumers to compensate for the the lack of intraspecific interference among the consumers and the large rate at which the consumers encounter the resource.

7.9.8 The Effect of Harvesting Both Species in the Resource-Consumer Subsystem

According to Theorem 5.9,

1. In the case where the consumers are trying to invade the system at $\left(\left(\frac{r_R - H_R}{r_R}\right) K_R, 0\right)$:

   (a) if $H_C < r_C$ then the consumers can invade for any level H_R of harvesting of the resource. The reason for this is that the rate of harvesting on the consumers is less than the consumers' intrinsic growth rate, so the consumers do not need to feed upon the resource in order to grow.

(b) we have that

$$
\begin{cases}
H_R < r_R \\
H_C < r_C + \frac{\alpha_{RC}}{h_{RC}}\left(\frac{e_{RC}(r_R-H_R)K_R}{\frac{r_R}{h_{RC}}+e_{RC}(r_R-H_R)K_R}\right)
\end{cases}
$$

$$
\Leftrightarrow \begin{cases}
H_R < r_R\left(1 - \frac{H_C-r_C}{e_{RC}K_R[\alpha_{RC}-(H_C-r_C)h_{RC}]}\right) \\
H_C < r_C + \frac{\alpha_{RC}}{h_{RC}}
\end{cases}
$$

But $r_C + \frac{\alpha_{RC}}{h_{RC}}\left(\frac{e_{RC}(r_R-H_R)K_R}{\frac{r_R}{h_{RC}}+e_{RC}(r_R-H_R)K_R}\right) < r_C + \frac{\alpha_{RC}}{h_{RC}}$ and $r_R\left(1 - \frac{H_C-r_C}{e_{RC}K_R[\alpha_{RC}-(H_C-r_C)h_{RC}]}\right) < r_R$. So there is a tradeoff in the amount of harvesting that can be done on each species. If $H_C > r_C + \frac{\alpha_{RC}}{h_{RC}}\left(\frac{e_{RC}(r_R-H_R)K_R}{\frac{r_R}{h_{RC}}+e_{RC}(r_R-H_R)K_R}\right)$ then the maximum value of H_R must be smaller than the case where $H_C < r_C + \frac{\alpha_{RC}}{h_{RC}}\left(\frac{e_{RC}(r_R-H_R)K_R}{\frac{r_R}{h_{RC}}+e_{RC}(r_R-H_R)K_R}\right)$. Similarly, if $H_R > r_R\left(1 - \frac{H_C-r_C}{e_{RC}K_R[\alpha_{RC}-(H_C-r_C)h_{RC}]}\right)$ then the maximum value of H_C must be smaller than in the case where $H_R < r_R\left(1 - \frac{H_C-r_C}{e_{RC}K_R[\alpha_{RC}-(H_C-r_C)h_{RC}]}\right)$. Biologically this tells us that if we have a sufficiently large amount of harvesting on the consumers, then we must have less harvesting on the resource. Conversely, if we have a sufficiently large amount of harvesting on the resource, then we must have less harvesting on the consumers. The reason for this is that harvesting the resource reduces the amount of food available to the consumers. If the consumers' food supply is shrinking because the resource is being harvested more, then the consumers cannot withstand being harvested as much. Similarly, if the consumers are being harvested more, they need more food to help sustain themselves so the resource cannot be harvested as much.

2. In the case where the resource is trying to invade the system at $\left(0, \left(\frac{r_C-H_C}{r_C}\right)K_C\right)$

(a) if $e_{RC} < r_R e_C h_C$ and $H_R < r_R - \frac{e_{RC}}{e_C h_C}$ then the resource can invade for any

level H_C of harvesting on the consumers. In this case, the consumers do not attack the resource at a high rate compared to the resource's intrinsic growth rate and the rate at which consumers exhibit intraspecific interference. The resource also is not harvested at a very high level. So harvesting the consumers is not needed in order to facilitate invasion by the resource. If $e_{RC} < r_R e_C h_C$ and $r_R - \frac{e_{RC}}{e_C h_C} < H_R < r_R$ then the consumers do no attack the resource often but there is a sufficiently large amount of harvesting on the resource. In this case, we need $H_C > r_C \left(1 + \frac{r_R - H_R}{K_C[e_C h_C (r_R - H_R) - e_{RC}]}\right)$ in order to reduce the amount of predation on the resource by the consumers by enough to allow the resource to invade the system.

(b) if $H_C > r_C \left(1 + \frac{r_R - H_R}{K_C[e_C h_C (r_R - H_R) - e_{RC}]}\right)$, $e_{RC} > r_R e_C h_C$, and $H_R < r_R$ the the resource is not harvested very much, although the consumers attack the resource at a high rate compared to the resource's intrinsic growth rate and the level of intraspecific interference the consumers exhibit. But, there is a sufficiently large amount of harvesting on the consumers, which suppresses their population level sufficiently to allow the resource to invade the system.

7.9.9 The Effect of Harvesting the Consumers in the Full Model

According to Theorem 5.14, if $H_C < r_C \left(1 - \frac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P\right)}\right)$ and $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ then increasing H_C makes it easier for the resource to invade if $e_{CP} h_{PC} < e_P h_P$ and harder to invade if $e_{CP} h_{CP} > e_P h_P$. If $m_P > \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ or if $m_P < \frac{1}{2}\frac{\alpha_{CP}}{h_{CP}}$ and $H_C > r_C \left(1 - \frac{m_P}{e_{CP} K_C \left(\frac{1}{2}\alpha_{CP} - h_{CP} m_P\right)}\right)$ then increasing H_C makes it easier for the resource to invade. In all cases, increasing H_C makes exclusion harder.

Biological Remark: It seems that increasing H_C should reduce the number consumers who can feed upon the resource and should reduce the number of consumers

who the predators can feed upon. This decrease in both the consumer and resource population should both make it easier for the resource to invade and harder for the resource to be excluded. This is the situation in most cases. However, when $e_{CP}h_{PC} > e_P h_P$, the consumers spend a sufficient amount of time avoiding the predators. Increasing H_C reduces the amount of consumers, which increases the predators' dependence on the resource for survival. This makes it harder for the resource to invade.

7.9.10 The Effect of Harvesting the Predators in the Full Model

According to Theorem 5.18, if $\frac{1}{2}\alpha_{RP}e_{RP}K_R - (m_P + H_P)(1 + e_{RP}h_{RP}K_R) > 0$ and $e_{CP}\alpha_{RP} >> \alpha_{RC}e_{RC}$ then increasing H_P makes it harder for the consumers to invade.

Biological Remark: Increasing H_P reduces the number of predators who can consume the consumers. It seems that this should make it easier for the consumers to invade and harder for them to be excluded. This is the situation in all cases, except when H_P is sufficiently small and $e_{CP}\alpha_{RP} >> \alpha_{RC}e_{RC}$. In this case, the mechanism is the same as the case when increasing m_P makes it harder for the consumers to invade the unharvested system. What is particularly interesting about the present case is that, as we can see from the analysis of the case of increasing m_P in the unharvested system, harvesting the predator population can actually increase the predator population for sufficiently small amounts of harvesting.

Chapter 8

Conclusions

In this paper, we used a model for intraguild predation to study the effects of harvesting on ecological communities. The model was derived in Chapter 2 using a time budget analysis similar to Holling [32] and Beddington [8]. We derived Beddington-DeAngelis-type functional responses for all the interactions, which include interference competition in additional to the usual Beddington-DeAngelis terms. In our model, we assumed the consumer species has an alternative food source which is not shared by the predator species, which we modeled by assuming the consumer species grows logistically in absence of the resource and predator species.

In Chapter 3, we looked at the 2-dimensional subsystems. In particular, we studied the $R - C$ subsystem, which was a predator-prey system with Beddington-DeAngelis functional response and both species growing logistically in the absence of the other species. By looking at the isoclines, we found conditions under which there are zero, one, two, or three interior equilibria. We used geometric and analytical techniques to find the local stability type of the equilibria and found a case in which there is an Allee Effect. We also found that if $\frac{e_{RC}K_C}{r_R} < 1 + e_C h_C K_C$ (in dimensionalized parameters), where e_{RC} is the rate at which the consumers attack the resource, K_C is the consumers' environmental carrying capacity, r_R is the resource's intrinsic growth rate, e_C is the rate at which consumers interfere with each other, and h_C is the

time consumers spend interacting with each other, then the $R - C$ subsystem is permanent and determined a sufficient condition for the interior equilibrium (R^*, C^*) to be globally asymptotically stable. We saw that the $R - C$ subsystem under goes a saddle-node bifurcation for the nondimensionalized parameter e_{RC} and a subcritical Hopf bifurcation as the nondimensionalized parameter h_C changes.

In Chapter 4, we looked at the full system. Though we did not determine the interior equilibria or the local or global dynamics due to the prohibitively complicated expressions involved in such analysis, we did find conditions under which the system is permanent. A sample of the kinds of dynamics possible when the system is permanent is shown in Figure 8.1. Here, we borrow parameter values from [61]. Through it is a little difficult to see in Figure 8.1a, we can see from Figure 8.1b that we have periodic behavior in this case.

We used sub- and supersolutions to get bounds on the size of the equilibria and used these bounds to determine sufficient conditions under which each species could either invade or be excluded from the system. Using these conditions, we were able to determine how invasibility and exclusion are affected by certain parameters.

The results of our parameter dependence analysis show that many different possibilities exist and that in many cases, changing the parameters sometimes makes invasion or exclusion easier and in other cases it makes invasion or exclusion harder. Typically, the affect of changing the parameters depends on other parameter combinations. Our anlaysis also yielded some unexpected results. We found that increasing e_{CP} makes it easier for the resource to be excluded if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P(1 + e_{CP}h_{CP}K_C) > 0$ and $e_{RC} >> e_{RP}$, where α_{CP} is the conversion efficiency from consumers to predators, e_{CP} is the rate at which the predators attack the consumers, m_P is the predators' natural mortality rate, h_{CP} is the time the predators spend handling attacked consumers, and e_{RP} is the rate at which the predators attack the resource. Because the consumers attack the resource more than the predators attack the resource, it seems
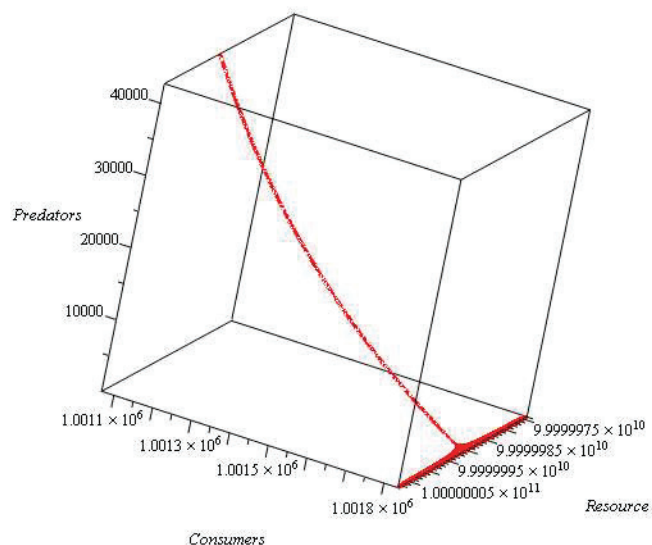
(a) Simulation of system (2.18) with $r_R = 1.36$, $r_C = 1.36$, $K_R = 1 \times 10^{11}$, $K_C = 1 \times 10^6$, $e_{RC} = 0.20$, $e_{CP} = 0.30$, $e_{RP} = 0.45$, $e_C = 0.05$, $e_P = 0.05$, $h_{RC} = 80$, $h_{CP} = 22$, $h_{PC} = 60$, $h_{RP} = 25$, $h_C = 30$, $h_P = 10$, $\alpha_{RC} = 0.2$, $\alpha_{CP} = 0.15$, $\alpha_{RP} = 0.2$, $m_P = 0.0065$, $H_R = H_C = H_P = 0$, $100 \le t \le 4500$
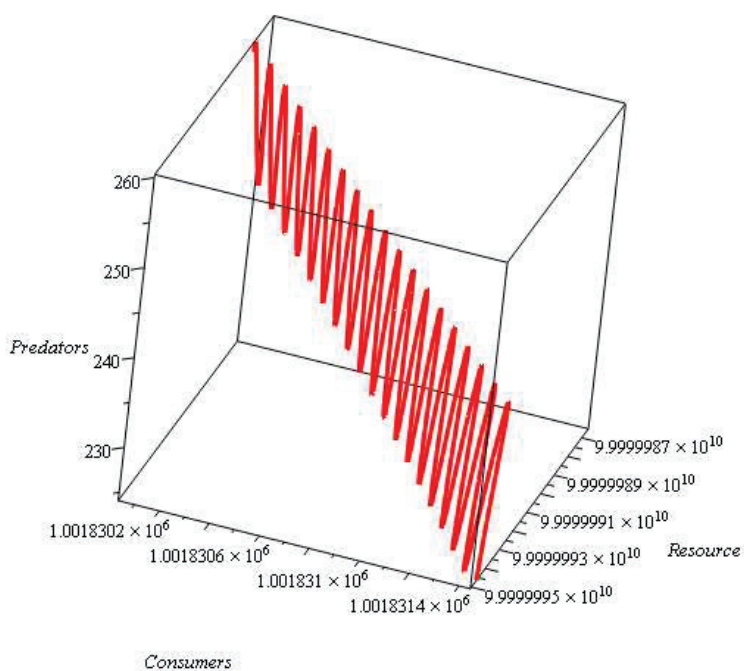
(b) Same parameter values as Figure 8.1a, except with $1000 \le t \le 1100$

Figure 8.1: *Sample dynamics possible when the system is permanent.*

that the more the predators attack the consumers, the harder it should be for the resource to be excluded. We also found parameter combinations under which having $e_{RC} << e_{RP}$ makes it easier for the resource to invade and $e_{RC} >> e_{RP}$ makes it harder for the resource to invade. In the case where the consumers are trying to invade the system, we found a situation in which increasing m_P made invasion harder. When the predators are trying to invade the system, we found discovered that under certain conditions, enriching the environment for the resource makes invasion harder. We also found that under most conditions, enriching the environment for the consumers makes it easier for the predators to be excluded provided that $\alpha_{RP}e_{RP} >> \alpha_{CP}e_{CP}$ and harder for the predators to be excluded if this condition was reversed. But we also found a case where increasing the environmental productivity for the consumers makes it easier for the predators to be excluded without this condition.

In Chapter 5, we look at how harvesting affects the system. Because of our choice of constant effort harvesting, there are no new dynamics as a result of harvesting. Instead, harvesting can move us in parameter space and therefore, can put in a different dynamic regime. We begin by looking at harvesting each or both species in each of the subsystems. We found that if we harvest only the consumers in the $C - P$ subsystem, it is necessary for K_C to be larger than in the non-harvested case. We also found that for intermediate values of H_C, the predators can be driven to extinction while the consumers remain viable. In the $C - P$ subsystem when we harvest both species, we discovered that there is a tradeoff in the amount of harvesting that can be done on each species in order to have coexistence. If we are allowed to harvest the predators at a sufficiently high rate then we must harvest the consumers at a sufficiently low rate. The opposite is also true. In the $R - C$ subsystem, we found that a sufficiently large amount of harvesting of the consumers can lead to coexistence and a sufficiently small amount of harvesting of the consumer can lead to resource extinction. In the case where both species are being harvested, there is a tradeoff in

the amount of harvesting that can be done on each species while having coexistence.

In studying the effects of harvesting on the full model, we found that under some conditions, harvesting the resource makes it easier for the consumer to invade and under other conditions, harvesting the resource makes it harder for the consumers to invade. Similarly, sometimes harvesting the resource makes it is easier for the consumers to be excluded from the system and other times it makes it harder for the consumers to be excluded from the system. We found that when R^* is bounded below by 0, increasing H_R makes it easier for the predators to invade the system and easier for them to be excluded from the system. By harvesting the consumers in the full system, we found that typically makes it easier for the resource to invade the system and makes it harder for them to be excluded. But we also found that if $\frac{1}{2}\alpha_{CP}e_{CP}K_C - m_P\left(1 + e_{CP}h_{CP}\left(\frac{r_C - H_C}{r_C}\right)K_C\right) > 0$ and $e_{CP}h_{PC} > e_P h_P$ then harvesting the consumers makes it harder for the resource to invade. When we harvested the predators in the full system, we found that can help or hurt the resource, depending on certain combinations of parameters. We also found that harvesting the predators helps the consumer species in most cases, although there is a case in which harvesting the predators makes it harder for the consumers to invade. In this case, we found that harvesting the predators can actually increase the predator population, at least if the predators have a sufficiently low natural mortality rate and the harvesting rate remains sufficiently small.

In Chapter 6, we explored a linear food chain, resource competition, apparent competition, and interspecific killing as special cases of intraguild predation where certain attack rates are set to zero. We studied how the invasibility and exclusion conditions of each species in each ecological community are different from intraguild predation. In some cases, we found invasibility and/or exclusion to be easier than in intraguild predation and in other cases, we found it to be harder. We also looked at harvesting in each type of community. Sometimes harvesting had the same effect on

the ecological community and other times it did not.

In Chapter 7, we looked more closely at the mechanisms behind some of the parameter dependencies we saw in the previous chapters. We highlighted some of the most interesting cases in the last section of the chapter. In some instances we were able to explain the underlying mechanism. In other cases we were able to take reasonable stab at the mechanism, though there could be some other mechanism at work than the one proposed. And in still other cases, the mechanism driving the observed parameter dependency could not be explained. We believe these cases are the most interesting cases and hope they lead to further investigation.

Other avenues for further investigation include relaxing some of the simplifying assumption made for analytical tractability such as having constant effort harvesting. It would also be interesting to associate empirical data with the model in order to be able to explore certain situations in more detail. This could permit us to find more numerical results. Even without data, further exploration of cases on the edge between two results, perhaps through computer simulations, could be enlightening. It has been shown that space can play a role in intraguild predation and can be an important consideration. The effects of spatial heterogeneity on intraguild predation have been looked at in [4, 5], the role of consumer and predator dispersal in [7], and cross-diffusion where consumers disperse conditionally to avoid areas of high predation in [57]. Additionally, there are other biological and bioeconomic factors, such as size structure, mutual predation, and the costs associated with harvesting, which remain to be studied.

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