MODELLING INTRAGUILD PREDATION WITH ADAPTIVE BEHAVIOUR

by

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Abstract

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The thesis examines the dynamics of intraguild predation models incorporating adaptive behaviour. The top predator varies its relative consumption of the intermediate consumer and the basal resource. The consumer alters its activity level in response to the threat of predation. Incorporating these adaptive behaviours facilitated three species coexistence, but restricted omnivory by promoting the formation of three species food chains. Model modifications which promoted omnivory also tended to reduce three species coexistence. It is predicted that omnivory should be most common when the intermediate and the basal species are similarly profitable to the predator. The model also predicts two types of omnivory. Strong omnivory occurs when the predator always consumes intermediate amounts of both prey items. Weak omnivory occurs when the predator preys almost exclusively on one prey at most times, but rapidly switches to include the other when the relative abundance of that second prey exceeds a certain level.
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Introduction

Omnivory is defined as the act of feeding on more than one trophic level (Pimm and Lawton 1978). There has been some debate regarding how frequently omnivory is observed in nature, with views ranging from the assertion that omnivory is rare (Pimm and Lawton 1978) to the belief that it is nearly ubiquitous (Polis et al. 1989; Arim and Marquet 2004). Early theoretical models of omnivory have shown that the addition of omnivorous links to simple food chains tends to reduce their stability (Pimm and Lawton 1978; Pimm and Rice 1987), creating limit cycles (Holt and Polis 1997) and, in some cases, producing chaos (Tanabe and Namba 2005). This would seem to suggest that occurrences of omnivory should be rare. However, numerous instances of omnivory have been documented in natural communities (Pimm and Lawton 1978; Polis et al. 1989; Arim and Marquet 2004) and other theoretical studies have suggested that omnivory can be stabilizing (McCann and Hastings 1997; Vandermeer 2006). The current view is that omnivory is common in nature (Yodzis 1984; Polis et al. 1989) and should be taken into account when dealing with management or conservation issues (Polis and Holt 1992). Nevertheless, the lack of quantification of interaction strength in natural communities means that it is possible that most omnivory is so weak that it has little impact on system dynamics.

One of the simplest configurations of omnivory consists of a top predator, an intermediate consumer and a basal resource that is fed upon by both the consumer and the predator. This food chain combines both predation and exploitative competition. Polis et al. (1989) call this type of interaction “intraguild predation” (IGP). It is distinguished from classical competition by the fact that one of the competitors (the predator) directly gains energy by
consuming its competitor. IGP also differs from traditional predation by having two pathways by which the top predator affects the consumer and vice versa. One of the consequences of these extra pathways of interaction is that population dynamics can be more complex than either competition or predation alone (Polis et al. 1989).

In spite of the discrepancy between predictions regarding the rarity of omnivory based on mathematical models and the observation of abundant omnivory in empirical studies, modelling of omnivorous food webs has given certain insights into the characteristics of natural systems. One of the most important insights from mathematical analysis of 3-species omnivorous systems is that, according to simple models, stable coexistence of all three species requires that the intermediate consumer must be a better competitor for the common resource than the top predator in order to avoid to extinction (Holt and Polis 1997). Another criterion for the possibility of coexistence is intermediate levels of productivity. At high levels of basal resource productivity (usually modeled as resource intrinsic growth rate or carrying capacity), the effect of predation becomes dominant and the top predator excludes the intermediate consumer; while at low productivity, competition is dominant and the consumer persists (Holt and Polis 1997; Diehl and Feissel 2000; Mylius et al. 2001).

Recently, more sophisticated models have been introduced to explain the widespread nature of omnivorous food webs. McCann and Hastings (1997) found that adding omnivorous links to a simple food chain adds to local stability, although this effect may only be limited to cases where the strength of the link is weak (McCann et al. 1998), and the chain without omnivory is unstable. Holt and Polis (1997) suggested that adaptive behaviour may facilitate
coexistence. They proposed that adaptive foraging, which allows the top predator to switch between the basal resource and the intermediate consumer, should stabilize the system. Singer and Bernays (2003) argued that an understanding of the causes and consequences of omnivory requires an understanding of the underlying foraging behaviour and Uchida et al. (2007) found that adaptive foraging has a stabilizing effect on small populations.

Krivan (2000) incorporated the effects of predator behaviour into two Lotka-Volterra models that assumed a trade-off between predation and competition. He found that prey switching by the omnivore can greatly expand the region of stable coexistence towards higher levels of resource productivities and intraguild predation can be a stabilizing factor if the productivity is high enough. However, an optimally foraging intraguild predator would eventually focus exclusively on the intraguild prey and the food web topology would become a strict tri-trophic food chain at high carrying capacities. His models assumed that feeding on the basal resource and middle consumer required mutually exclusive foraging modes on the part of the top predator (i.e. searching in different microhabitats, use of different foraging strategies, morphological differences). However, predators often do not have mutually exclusive searching behaviours for different prey types.

Krivan and Diehl (2005) tried to address this problem and assumed that their omnivore followed the optimal diet rule where a less profitable prey is included or dropped from the diet depending on the relative density of more profitable prey (Werner and Hall 1974). With their model, they found the overall positive effect on stability of adaptive omnivory to be relatively small. Moreover, they found that this facilitation required that the intermediate
consumer be a more profitable prey type than the basal resource for the top predator. If this condition is met, the range of parameter space permitting persistence of all 3 species expands, and the region where the consumer excludes the omnivore shrinks. However, by using the diet rule in their model, they assumed there was no trade-off between the omnivore’s ability to feed on its two food type. Also, this model formulation prevented the omnivore from completely dropping the more profitable prey, no matter how low its density. These limitations may restrict the applicability of their model.

All the models discussed above treat the omnivore’s feeding decision as an either-or process, and have assumed the switch between feeding modes to be instantaneous. It is likely that the resource and the consumer both make up a portion of the predator’s diet at any given time and the relative proportions of the resource and consumer in that diet changes gradually depending on their abundance. Ma, Abrams, and Brassil (2003) and Abrams and Matsuda (2004) have shown that models with non-instantaneous prey switching can produce very different results from ones with instantaneous switching. Thus, a predator’s degree of omnivory might be better modelled as a continuous trait or strategy. In many ways, this would be analogous to one predator, two prey models where the predators have a choice to be a generalist or to specialize on one of the two prey. There have been many examples in the literature where prey choice is modelled as a predator trait with potential trade-offs.

In recent years, the potential population dynamical consequences of adaptive anti-predator behaviour have received a lot of attention. In their 2003 review, Werner and Peacor find that there is strong evidence for significant population dynamical effects of such behaviour.
There is strong empirical evidence that prey species change their foraging behavior in response to predators (Schmitz 1998; Schmitz and Suttle 2001; Trussell et al. 2003; Brodin and Johansson 2004). Lima (1998) reviews 70 studies, demonstrating activity change in a wide range of taxa following exposure to predator. However, such prey adaptation has not yet been considered for omnivorous systems. Although Diehl (1995) suggested that prey refuges can contribute significantly to the survival of the intermediate consumer. One of the goals of this thesis is to explore the effects of the intermediate consumer’s predator avoidance behaviour on the persistence of omnivorous food webs.

Holt and Polis (1997) had suggested that both types of behaviour might help explain the persistence of omnivorous systems, but there have apparently been no subsequent analyses of models in which both types of behaviour are present. Such a model requires a method of modelling the interacting behaviors of two species. An approach to modelling trait changes in a population was proposed in Abrams et al. (1993), and further developed in Abrams and Matsuda (2004). This framework assumes that species adaptively adjust their traits based on fitness landscape climbing functions similar to ones used in describing adaptive dynamics in evolutionary models. I applied this modelling method to a three species food web with intraguild predation, where the top predator and the intermediate consumer both exhibit adaptively plastic traits related to foraging behaviours. With this model, I hope to answer several questions regarding the nature of omnivorous food webs: (1) does the inclusion of predator behaviour, consumer behaviour or a combination of both facilitate three species coexistence, (2) is having consumer be more profitable than the resources still required for coexistence based on this model formulation, (3) does the rate of behaviour change affect
coexistence, (4) how are the answers to the preceding three questions affected by the use of alternative models that include factors such as non-linear predator trade-offs and minimum predation rates.

**General Monomorphic Model**

I begin by considering a general model of the simple three species IGP food chain described in Polis et al. (1989) consisting of a resource (R), consumers (C), and a top predator (P). However, unlike Polis et al. (1989) I consider a case where both the consumer and predator species exhibit variable traits. The top predator may feed on either the consumer and/or the resource. The resource grows according to logistic growth with intrinsic growth rate $r$ and a carrying capacity of $K$. The consumer and top predator are assumed to exhibit satiation and thus assumed to have Holling type II functional responses (Holling 1959), with the top predator having the multi-species version of this response. This type of response is found to be more realistic than a linear response (Uchida et al. 2007) and is the model used in Krivan and Diehl (2005). The differential equations describing the population dynamics are:

$$R' = R[r(1 - \frac{R}{K}) - \frac{\lambda_{RC}(w)C}{1 + h_{RC}\lambda_{RC}(w)R} - \frac{S_{RP}(u)\lambda_{RP}P}{1 + h_{RP}S_{RP}(u)\lambda_{RP}R + h_{CP}S_{CP}(u)\lambda_{CP}(w)C}]$$  \hspace{1cm} (1a)$$

$$C' = C[\frac{e_{RC}\lambda_{RC}(w)R}{1 + h_{RC}\lambda_{RC}(w)R} - \frac{S_{CP}(u)\lambda_{CP}(w)P}{1 + h_{RP}S_{RP}(u)\lambda_{RP}R + h_{CP}S_{CP}(u)\lambda_{CP}(w)C} - m_c]$$  \hspace{1cm} (1b)$$

$$P' = P[\frac{e_{RP}S_{RP}(u)\lambda_{RP}R + e_{CP}S_{CP}(u)\lambda_{CP}(w)C}{1 + h_{RP}S_{RP}(u)\lambda_{RP}R + h_{CP}S_{CP}(u)\lambda_{CP}(w)C} - m_p]$$  \hspace{1cm} (1c)$$

The behavioural traits of the predator and consumer are characterized by the variables $u$ and $w$ respectively. The parameter $\lambda_{ij}$ is the capture rate of species $i$ by species $j$. The function $s_{RP}$ is the predator preference function, which modifies the capture rate of the resource by the
predator. The adaptive variable \( u \) determines the value of this term, and also the term \( s_{CP} \), which similarly modifies the predator’s capture rate of the consumer. This model assumes that capture rates (\( \lambda \)) and predator preference (\( s \)) are independent of one another and their interaction is a strict multiplicative combination. The parameter \( e_{ij} \) is the conversion efficiency of food type \( i \) into new individuals of species \( j \), \( h_{ij} \) is the handling time species \( j \) spends on an item of food type \( i \), and \( m_i \) is the density independent mortality rate of species \( i \).

In order to simplify the model, I assumed the predator’s preference functions to have a simple linear form for the majority of the analysis presented here; the predator’s maximum capture rate of the consumer (for a given consumer behaviour) is multiplied by the variable \( u \), and conversely, \( 1-u \) multiplies the predator’s maximum capture rate of the basal resource. Non-linear trade-offs between the two preferences will be considered in later sections. The capture rate (per unit resource density) of the resource by the consumer (\( \lambda_{RC} \)) and consumer by the predator (\( \lambda_{CP} \)) are both functions of the variable \( w \), which represents the activity level of the consumer. The variable is also bounded between 0 and 1, with 0 representing a non-active consumer and 1 representing the consumer at maximal activity. The two traits, \( u \) and \( w \), change as an increasing function of the derivative of the species’ per capita growth rate with respect to individual trait value. This is similar to the fitness landscape climbing functions used by Abrams and Matsuda (2004, 2005) to model trait changes.

\[
\begin{align*}
    u' &= v_p \left[ \frac{\partial f_p(u_{mut}, u_{res})}{\partial u_{mut}} \right] + z(u) \quad (2a) \\
    w' &= v_c \left[ \frac{\partial f_c(w_{mut}, w_{res})}{\partial w_{mut}} \right] + z(w) \quad (2b)
\end{align*}
\]
The function \( f_i(u) \) is the instantaneous per capita growth rate of a "mutant" individual of species \( i \) (where \( i = C \) or \( P \)). Here, 'mutant' denotes a variant trait value held by a small number of individuals, and does not necessarily mean that the individual in question is genetically different from others. The subscript "res" similarly denotes the mean behavior of the rest of the population in most cases, but does not necessarily imply the existence of a genetic polymorphism. Because the form of the trait dynamic equations is basically similar to a simplified model of quantitative genetic change (Abrams et al., 1993), and the evolutionary models of 'Adaptive Dynamics' (Geritz et al., 1998), it can also be used to represent evolutionary change with appropriate parameter values. The parameter \( v_i \) is a scaling constant that describes how quickly species \( i \) can alter its trait value. High values of \( v_i \) allow the trait to change significantly over relatively short time scales (i.e., within the individual’s lifetime). Such values can be used to model trait changes due to factors such as behavioural changes or phenotypic plasticity. Low values of \( v_i \) model evolutionary change (Abrams et al. 1993). The function \( z \) reflects the behavioural sampling or mutational bias near extreme trait values (0 or 1) which pushes the value away from the extreme. This function has the required effect of preventing trait values from crossing the biologically defined boundaries of 0 and 1. The form of the function used in the analyses reported here is:

\[
z(x) = \frac{\varepsilon}{x^2} - \frac{\varepsilon}{(1 - x)^2}
\]  

(2c)

where \( \varepsilon \) is a very small constant. When \( x \) is near 0, \( z \) is positive and when \( x \) is near 1, \( z \) is negative. It is possible that the \( z \) function for predators and consumers could have different forms and it is likely that the value of the constant \( \varepsilon \) is different for the two species; however, to simplify the model, I assumed both species have the same \( z \) function and the same value of
This assumption is not likely to affect the dynamics significantly. The full form of equation (2a) and (2b) is shown below (the terms within the parenthesis are the result of the differentiation of the per capita growth rate of the species with respect to its behaviour):

\[
\begin{align*}
    u' &= v_p \left( \frac{C_{cp}^{'}(u)\lambda_{cp}(w)(e_{cp} + R\lambda_{cp}^{'}(w)h_{cp} - e_{rp}h_{rp}) + R\lambda_{cp}^{'}(w)S_{cp}(u)(e_{cp}h_{cp} - e_{cp}h_{rp})}{(1 + R\lambda_{cp}^{'}(w)h_{cp}S_{cp}(u) + C\lambda_{cp}^{'}(w)h_{cp}S_{cp}(u))^2} \right) + \frac{\varepsilon}{u^2} - \frac{\varepsilon}{(1-u)^2} \\
    w' &= v_c \left( \frac{P_{cp}(u)\lambda_{cp}^{'}(w)}{1 + S_{cp}^{'}(w)R\lambda_{cp}^{'}(w)h_{cp} + C\lambda_{cp}^{'}(w)h_{cp}) + \frac{\varepsilon}{w^2} - \frac{\varepsilon}{(1-w)^2} \right),
\end{align*}
\]

where primes denote derivatives with respect to the variable of the functions in question. As noted above, the preference function controls the predator's capture rate of consumers and resources. I described the linear form of this function above. This is an example of the more general power function:

\[
\begin{align*}
    S_{cp}(u) &= u^n \quad (3a) \\
    S_{rp}(u) &= (1-u)^n \quad (3b)
\end{align*}
\]

where \(n\) is a positive exponent and \(u\) is the index of preference for the consumer.

The consumer's activity level directly influences both its food intake and vulnerability to predators. For this model, I assumed the per capita capture rate of resource by consumers \(\lambda_{cp}\) is a decelerating function of activity level to model the eventual diminishing returns of increased foraging time. The capture rate of consumers by predators \(\lambda_{cp}\) is an accelerating function of the consumer’s activity, and represents the greater vulnerability of a more active forager. A minimum rate of capture is included in both functions to represent a baseline.
vulnerability of consumers to predators and resources to consumers respectively. The model has the following form:

$$\lambda_{CP} = (\lambda_{CP_{max}} - \lambda_{CP_{min}})W^a + \lambda_{CP_{min}} \quad (4a)$$

$$\lambda_{RC} = (\lambda_{RC_{max}} - \lambda_{RC_{min}})W^{\frac{1}{b}} + \lambda_{RC_{min}} \quad (4b)$$

The parameters $a$ and $b$ are positive constants greater than 1 that characterize the curvature of their respective functions; the parameter $\lambda_{CP_{min}}$ represents the minimum vulnerability of the consumer to predators and the parameter $\lambda_{RC_{min}}$ represents the minimum foraging ability of consumers on resources. Here, I assume that a completely inactive consumer would be unable to obtain any resource and set the baseline foraging parameter $\lambda_{RC_{min}}$ to zero. The parameters $\lambda_{CP_{max}}$ and $\lambda_{RC_{max}}$ represent the maximum values of the functions. The model is not sensitive to the exact form of equations (4a,b). A number of other functions that lead to a positive curvature (i.e. positive second derivative) for $\lambda_{CP}$ and a negative curvature for $\lambda_{RC}$ were explored, and all produced qualitatively similar results. One of the alternate functions examined in place of equation 4a was an exponential function of the form:

$$\lambda_{CP} = \frac{(\lambda_{CP_{max}} - \lambda_{CP_{min}})(e^{aw} - 1) + \lambda_{CP_{min}}(e^a - 1)}{(e^a - 1)} \quad (4c)$$

where the parameter $a$ is a positive constant greater than 1 that characterizes the curvature of the function between $w=0$ and $w=1$. An alternate function examined for the capture rate of resource by consumer is the saturating function:

$$\lambda_{RC} = \frac{(\lambda_{RC_{max}} - \lambda_{RC_{min}})(b + 1)w}{b + w} + \lambda_{RC_{min}} \quad (4d)$$
where b is a positive constant less than 1 characterizing the curvature of the function. The results produced by using these two functions are similar to those produced by functions 4a and 4b.

**Analysis of Parameter Space for Coexistence**

There are a large number of parameters in this model. A list of the parameters and their definitions can be found in Table 1. The parameters examined in greatest detail are the resource carrying capacity, $K$, and the predator mortality, $m_P$, because those have been shown previously (Holt and Polis 1997) to affect the qualitative nature of the dynamics of an IGP system even in the absence of any handling time or any adaptive change in feeding behavior. These parameters are also the main determinants of stability in simple predator-prey models that are capable of exhibiting cycles. These two parameters were also identified as the main determinants of the outcome of the 3-species interaction by Krivan and Diehl (2005). Predator mortality and resource carrying capacity are also likely to be the easiest parameters to manipulate experimentally (e.g. Diehl and Feissel 2000). Specific sets of the remaining parameters that are illustrated in Table 1 were chosen based on preliminary simulations, to represent the full range of dynamic behaviours observed in that preliminary set. For each of these sets of the other parameters, an analysis of system dynamics was performed for a two-dimensional parameter space of productivity ($K$) versus density independent predator mortality ($m_P$). The main goal was to determine how coupled behavioral change in predator preference ($u$) and consumer activity level ($w$) altered system dynamics and the regions of stability and of coexistence.
To investigate this three species omnivory system, I use the mutual invasibility definition of persistence where a system of species is considered to coexist if each of them can increase when rare. Under this criterion, for an omnivorous system to exist, mutual invasibility of top predator (P) and intermediate consumer (C) is a necessary, though not sufficient, condition for the existence of omnivory. (It is not sufficient because the adaptive optimum of the predator's trait may be to eat only consumers, turning the system into a food chain.) The basal resource (R) must be present if any other species is to survive. In theory, invasion need not imply coexistence (e.g. Abrams and Shen 1989, Case 1991, Meszena et al. 2006). However, simulations with greater initial densities of the invader species always produced the results expected from the invasion analysis. The analysis classifies a set of parameters by the type of community produced. Here the possibilities are: R only; R and C; R and P; R,C,P as a food chain; R,C,P as a competition system; and R,C,P as an IGP system. Within each type, the results are further classified by whether the system approaches a stable point equilibrium or not.

I first examine the ability of the predator to invade a system with only the basal resource and intermediate consumers. For this analysis, I assumed a linear predator choice function because it is the simplest case. Letting P=0, I solved for the region on the K vs. mP parameter space where consumers can exist and also solved for the equilibrium densities of the two populations where they existed. In the absence of predators, I assumed the consumers have maximal activity (w=1). This approximates the equilibrium value of w that is produced by the trait dynamic equations when predators are absent, although the zC
function forces the equilibrium value to be slightly less than 1. Under such assumptions, resource and consumers are present when:

\[
K > \frac{m_C}{\lambda_{RC_{max}} (e_{RC} - h_{RC} m_C)}
\]  

(5a)

Equation (5a), which I will call the consumer existence curve, can be represented as a vertical line on a plot of K vs. \(m_p\), to the right of which consumers are present. Within this region, the equilibrium density of the resource and consumer is:

\[
R^* = \frac{m_C}{\lambda_{RC_{max}} (e_{RC} - h_{RC} m_C)}
\]

(5b)

\[
C^* = \frac{r e_{RC} (K e_{RC} \lambda_{RC_{max}} - m_C (K h_{RC} \lambda_{RC_{max}} + 1))}{K \lambda_{RC_{max}}^2 (e_{RC} - h_{RC} m_C)^2}
\]

These equilibrium points exist when:

\[
m_C < \frac{e_{RC}}{h_{RC}}
\]

(5c)

and are stable if:

\[
K < \frac{e_{RC} + h_{RC} m_C}{h_{RC} \lambda_{RC_{max}} (e_{RC} - h_{RC} m_C)}
\]

(5d)

At high levels of productivity, where this inequality does not hold, the resource and consumer undergo limit cycles. Here I consider only the case where there are no limit cycles, allowing analytical results for predator invasion.

For the invading predators, their initial preference is assumed to be maximally for the consumers (\(u=1\)). Even though the \(z_P\) function would prevent the equilibrium value from reaching that value, the equilibrium should be close to \(u=1\). This choice of initial preference is based on the assumption that the energetic value of the consumer is high enough that a
small number of predators would have a greater success at invading a two species system by concentrating on the consumers. Using the equilibrium densities of resource and consumer, I determined parameter values for which the per capita growth rate of the predator was greater than zero, thus indicating the region in parameter space where predators can successfully invade. The condition is shown below:

\[ m_p < \frac{C^* e_{CP} \lambda_{CPmax}}{1 + C^* h_{CP} \lambda_{CPmax}} \]  

(5e)

Where \( C^* \) is the consumer equilibrium density as given by equation 5b. I will refer to this curve as the predator invasion curve. Where the population of densities of resource and consumers do not settle to an equilibrium but to a stable cycle, this condition is no longer valid and the ability of a predator to invade must then be determined numerically.

A similar analysis was performed for consumer invasion into a resource-predator only system. For this system, I assumed complete predator preference for the resource (\( u=0 \)), and that the invading consumer was completely active (\( w=1 \)). These assumptions are again reasonable because predators should prefer resources when that is all that is present, and the invading consumers will then initially experience little or no predation. The presence of the \( z \) function will again produce deviations from these ideal values, but the equilibrium values should be close to \( u=0 \) and \( w=1 \). With these assumptions, and in the absence of consumers, predators are present when:

\[ m_p < \frac{K \lambda_{RP} e_{RP}}{1 + K \lambda_{RP} h_{RP}} \]  

(5f)

I call equation (5f) the predator existence curve and within the region underneath this curve the equilibrium densities of the resource and predators are:
\[ R^* = \frac{m_p}{\lambda_{RP}(e_{RP} - h_{RP}m_p)} \] (5g)

\[ P^* = \frac{re_{RP}(Ke_{RP}\lambda_{RP} - m_p(1 + Kh_{RP}\lambda_{RP}))}{K\lambda_{RP}^2(e_{RP} - h_{RP}m_p)^2} \]

These equilibria exist and are stable if:

\[ m_p < \frac{e_{RP}}{h_{RP}} \] (5h)

and

\[ m_p > \frac{e_{RP}(Ke_{RP}\lambda_{RP} - 1)}{h_{RP}(Ke_{RP}\lambda_{RP} + 1)} \] (5i)

Within this region I can substitute the equilibrium densities of the resource and predator into the consumer growth equation. For the region with predator mortality less than the value given in equation (5i), the resource and predator cycle and this analysis is no longer valid.

Solving the consumer growth equation for \( m_p \) yields a threshold for consumer invasion:

\[ m_p > \frac{e_{RP}h_{RP}m_C}{\lambda_{RCmax}(e_{RC} - h_{RC}m_C) + \lambda_{RP}h_{RP}m_C} \] (5j)

This consumer invasion curve is independent of resource carrying capacity and is thus a horizontal line on the K-\( m_p \) plot above which invasion is possible.

Plotting the two species-pair existence curves (5a and 5f) and species invasion curves (5e and 5j) on the productivity-predator mortality parameter space divides the parameter space into five regions as shown in figure 1: (A) A resource-only region is found where productivity is low. (B) A resource-consumer region is found next to the R-only region; this zone of 2-species coexistence occurs where the productivity is high enough to support consumers but, where the productivity is still too low or the predator mortality is too high to allow predator
invasion. (E) Near the bottom of the graph, where predator mortality is very low, there is a resource-predator (RP) region where the predator can coexist with the resource, but where consumers are unable to invade. (C and D) Between the RP and RC region are the two regions where all three species can coexist. The larger region of these two (region C) represents parameters that allow the predator to successfully invade a system containing only resources and consumers, but do not allow the predator to survive with the resource alone. Below this coexistence region in (figure 1) is the smaller region (D) where both the predator and the consumer can survive alone on the resource and where both of the species can successfully invade when rare. Omnivory can only occur in regions C and/or D, but the invasion analysis cannot tell us what subset of regions C and D results in 3 species coexisting with the predator feeding on both resource and consumer (i.e., omnivory). Conclusions about the parameter space yielding omnivory will be drawn after incorporating the simulation results in the following sections.

The curves of the mutual invasion graph are highly sensitive to the behaviour of both predators and consumers during invasion. Deviation from the assumed behaviour (u=1, w=1 for predator invasion; u=0, w=1 for consumer invasion) increases the complexity of the equations for the invasion boundaries in parameter space. The shape of the curves is particularly sensitive to the predator’s behaviour. If the value of u during predator invasion is less than one, the predator invasion threshold drops, reducing the maximum predator mortality where the predator is able to invade. Conversely, if the value of u is greater than zero during the consumer invasion, the consumer invasion threshold changes from a horizontal line into a curve with a negative second derivative with respect to K. These shifts
in the invasion curves can greatly alter the regions where 3-species coexistence and omnivory are possible (refer to figures 2a and 2b). Because the sampling bias function prevents $u$ from reaching zero, it is expected that a curved consumer invasion threshold as depicted in figure 2b is more likely than the horizontal threshold presented in figure 1. Deviations from assumed consumer behaviour have similar but less noticeable effects. In general, any deviation from the assumed behaviour reduces the size of the regions where the rare species can invade, and thus reduces the size of the parameter space where three species coexistence is possible. These results suggest that, all else being equal, an adaptive predator provides a less restricted parameter space for three species coexistence since a non-adaptive predator obviously cannot adjust its behaviour to match the optimal invasion behaviours ($u=1$ for predator invasion, $u=0$ for consumer invasion) necessary to maximize the parameter space for three species coexistence.

The analysis above only holds for regions where the two species system comes to a stable equilibrium. If the stability conditions are violated, the two species system exhibits limit cycles and the use of equilibrium densities for calculating invasion success becomes invalid. In such cases, invasion can only be determined numerically. Using the parameter set in figure 1, a RC only system will come to a stable equilibrium if $K < 9.28$, which is less than 50% of the parameter space in figures 1 and 2. A RP only system will come to a stable equilibrium if $m_p > \frac{0.025(0.2K - 1)}{(0.2K + 1)}$. 
Numerical Integration

To examine the robustness of the analytical prediction and to analyze more complicated variations of the model, numerical integration of the model was necessary. The model was numerically integrated using Mathematica 5 (Wolfram Research, 2003) over a grid of values of resource carrying capacity and predator mortality. Carrying capacity was varied from 1 to 20 in steps of 0.1 and predator mortality was varied from 0.001 to 0.1 in steps of 0.001. At each combination of $K$ and $m_P$, the model was integrated for 10,000 time steps. The population levels of each species were averaged over the last 5,000 time steps and classified as either present or absent based on their population relative to the carrying capacity. The coefficient of variation was calculated for each of the species based on the last 5,000 time steps and the system was determined to be either at a stable equilibrium if the value of the c.v. was less than 0.01 or sustained fluctuations if the value was greater. Inspection of a large number of simulations suggested that 5000 time units was enough for the system to be very close to its attractor (its final pattern of dynamics). Inspection of the period of cycles also suggested that 5000 time units spanned a long enough time period to yield an accurate estimate of the mean and variance of population sizes. The typical length of a period of cycling populations was found to be between 50 to 200 time units for most of the range of parameters explored here. All final food web configurations were classified based on the species present and whether the population reached equilibrium or not. If all three species were present, the final system was further classified based on the average value of the predator’s preference. The system was classified as a three species food chain if $u > 0.99$, as a two species competition system if $u < 0.01$, and as an omnivorous system if $u$ was between these two values. The resulting zones in parameter space were plotted using SigmaPlot 9.0.
Three types of system were investigated. One was a scenario in which the consumer is more profitable to the predator than is the resource, reflected by:

$$\frac{e_{RP}}{h_{RP}} < \frac{e_{CP}}{h_{CP}}$$  \hspace{1cm} (6)

This scenario was based on the finding that omnivory in a system with predator diet choice required the intermediate consumer to be the more profitable food item for the top predator (Krivan and Diehl 2005). To verify whether this is a requirement for this model, I included a parameter set in which the profitabilities are equal and one where the consumer is slightly less profitable. A list of parameters and their values can be found in the tables section and in the legends of the model result figures.

2. Models in which only one species exhibits behavioural flexibility

Before delving into the general model, I examined two simpler versions of the model where there was only behavioural change in either the consumer or the predator, but not both. The analysis of these two models was done using numerical integration. Both of the models used a linear trade-off for predator preference and assumed a parameter set where the consumer is more profitable to the predator than is the resource (i.e. inequality (6) is satisfied).

In the first model, the predator is assumed to have fixed equal preferences for both consumer and resource (u=0.5) while consumer activity, w, is free to vary adaptively. There was no difference in the area of three species coexistence when compared to a model where consumer activity, w, is set to its maximum value of 1 (left panel of figure 3). However, by allowing the consumer to vary its activity level, a portion of the three species region at high
productivity became destabilized and changed from equilibrium dynamics in the non-adapting case to limit cycles in the adapting case (right panel of figure 3). This region of instability continues to enlarge as $K$ increases. Beyond $K = 20$, non-equilibrium dynamics dominate the three species region. Recall that, because the predator is assumed to have equal and fixed preferences, the entire 3-species area is characterized by omnivory. When predators are absent, there is no cost associated with increasing consumer activity and thus the consumer is always at its maximal activity level ($w=1$); conversely, when predators are present, consumers become less active when the resource carrying capacity increases or when predator mortality decreases (figure 4 shows the average value of $w$). This is expected because the predator population increases under both conditions and it is then adaptive for consumers to decrease their activity. When consumers are allowed to change their behaviour in the presence of predators, the consumer population is higher than if $w$ is held constant. Even where the consumers are cycling, the mean population is higher in the model with adaptive behaviour.

In the second simplified model, I allowed only the predator to change its behaviour. The consumers are assumed to have maximal activity ($w=1$) and the predator preference trade-off is linear ($n=1$). Compared to a model where predator preference is fixed at 0.5, the model with flexible behaviour produces a larger region of three species coexistence (figure 5). However, most of the expansion of the three species region was into the region of parameter space that previously was characterized by resource and consumers only. Thus, adaptive predator behaviour primarily increased the predator's ability to invade resource-consumer systems. Within the three species region, most of the area is classified as a three species food
chain. There are two small regions where the system is omnivorous. One omnivory region is
sandwiched between the three species food chain region and the resource-predator only
region. In this part of parameter space the system reaches a stable equilibrium and the
predator preference is at a constant, intermediate value. I call this strategy of consistently
consuming both prey items strong omnivory. In this region, the value of u drops very sharply
as predator mortality (m_P) decreases moving from the upper to the lower boundary of the
region. A second omnivory region is embedded inside the region with three species food
chain exhibiting non-equilibrium behaviour. In this omnivory region, the system acts like a
three species food chain most of the time, but periodically the predator alters its behaviour to
temporarily include the basal resource into its diet. This strategy, which I call weak
omnivory, is driven by population cycles of the resource and consumer (see figure 6). The
averaged final values of u are presented in figure 7.

3a. Both species adaptive; A linear predator preference trade-off (n=1); Consumer is
more profitable to the predator than is the resource

Returning to the general model in which both species exhibit adaptive behaviour, I first
considered the case where the trade-off in predator preference is linear (i.e. s_{CP}(u) = u; s_{RP}(u)
= 1–u) and where the consumer is more profitable than the resource.

The numerical integration results show six different regions of community composition
(figure 8). Where productivity is low, there is a resource only region. At high predator
mortality, there is a resource-consumer region and at very low predator mortality, there is a
resource-predator region. Between those two regions is the region of three species
coexistence which makes up about 54% of the total parameter space. This region is further divided up into three smaller regions based on the type of interaction between the three species. There is a large region where the system acts as a three species food chain; this makes up 88% of the three species parameter space and about 48% of the total parameter space. A smaller region beneath the food chain region is where the system is considered omnivorous; and this represents 11% of the three species parameter space and 6% of the total parameter space. Finally, between the omnivorous region and the resource-predator only region is a very narrow region where the interaction between the three species resembles and was classified as a stable two species competition system. Such a system initially seemed impossible since a two species competitive system with only one resource cannot exist at equilibrium (Abrams and Holt 2002). However, upon closer examination, the predator is found to be a very resource-focused omnivore (u<0.01) rather than a pure competitor for the basal resource. Even though the consumers are better competitors for the basal resource, they are unable to increase their population size and exclude the predators because this would then cause the predators to focus on them. This region is very small, making up less than 1% of the three species’ coexistence parameter space, and is essentially a transition zone between the omnivorous region and the resource-predator only region. Figure 9 shows the average final values of u and w for the basic model.

The position of the five major regions (excluding the tiny “competition” region) matches closely to the position of the five regions outlined in the analysis in the previous section. Of particular interest is the correspondence of the three species food chain region to the region where predators can invade a system of resource and consumers but cannot survive without
the consumers. Similarly the omnivorous region corresponds to the region where both the consumers and predators can survive alone with the resource and can also invade a system containing the other two species.

Four of the six regions (RC only, RP only, three species food chain, three species omnivorous) exhibited both equilibrium and non-equilibrium dynamics. The non-equilibrium systems can either be cyclic or chaotic. These regions of instability tend to occur at higher carrying capacity, but may also appear near the border between two different coexistence regions.

Compared to the simplified model where only the predator can alter its behaviour, the inclusion of adaptive consumer foraging/defense behaviour has produced a stabilizing effect on the system, reducing the size of the food chain region exhibiting non-equilibrium dynamics. This has the additional effect of eliminating the weak omnivory region. The consumer’s ability to change its activity level allows it to respond to variations in the population level of both the predator and the resource.

3b. Both species adaptive; A linear predator preference trade-off (n=1); Consumer and resource are equally profitable to the predator

The same analysis was performed using the parameter set in which the consumers and resource were equally profitable. This represents a reduction in the profitability of the consumer compared with the preceding analysis. Under these conditions, the results from the simulation showed a three species region that is about half the size of the three species region
in the previous model, taking up about 29% of the total parameter space (figure 10). The resource-predator region was greatly enlarged and the upper boundary of the three species region has also been lowered. However, within the three species region, the omnivorous region has increased its size and makes up 29% of the three species region, or 8.5% of the total parameter space. The “competition” region has significantly increased its size to 9% of the three species area, which is about 2.5% of the total parameter space. The remaining 62% of the three species region consists of food chain dynamics. This is equivalent to about 18% of the total parameter space.

There is also a new, small omnivory region that appears embedded within the unstable portion of the three species food chain region. This new region is similar to the weak omnivory region first observed in the model with where only the predator exhibits behavioural flexibility. The predator’s omnivorous behaviour is still driven by the population cycles of its two prey, but graphs of population dynamics with parameters drawn from this region showed that many of the systems within this region behave in a chaotic manner or with complex population cycles, unlike the simple cyclic dynamics of the earlier model.

3c. Both species adaptive; A linear predator preference trade-off (n=1); Basal resource more profitable to the predator

In order to further examine whether a more profitable consumer is required to produce omnivory, I simulated a model where the resource is slightly more profitable than the consumer. Numerical integration of this model shows a much larger resource-predator
region compared with both of the earlier parameter sets (figure 11). Also, the three species region has become much smaller, comprising less than 10% of the total parameter space. However, about 76% of this three species region is omnivorous, which is equal to about 7% of the total parameter space. At higher carrying capacity and higher predator mortality, the omnivory system becomes unstable and exhibits chaotic dynamics. There is a tiny region between the omnivory region and the resource-consumer region that is classified as a three species food chain, but it makes up less than 1% of the total parameter space. Note that this destabilization of dynamics at higher predator mortality contrasts with the situation in a simple predator-prey system (e.g., RC or CP, without adaptive behaviour) in which greater mortality is stabilizing.

3d. Both species adaptive; A linear predator preference trade-off (n=1); Investigating the effects of various handling times

To examine the effects of handling time on this basic model, I changed the value of \( h_{RP} \) and \( h_{CP} \) to one-half or twice of their original value in the simulation in section 3a while keeping the rest of the parameters the same. The results of changing the predator-consumer handling time are shown in figure 12. The left figure uses \( h_{CP} = 0.5 \), which is half of the original value, while the right figure uses \( h_{CP} = 2 \), which is twice the original value. Altering this handling time only affects the boundary between RC only and three species food chain region. A higher value of \( h_{CP} \) inhibits predator invasion into RC only areas but has no effect on the size or position of the omnivory or RP only regions. This is expected because a higher \( h_{CP} \) effectively reduces the energy gain per unit time by the predator when it eats a consumer. Conversely, altering the predator-resource handling time only affects the omnivory and RP
only region but has no effect on the upper portion of the three species food chain region. A reduction of $h_{RP}$ enlarges the omnivory region as well as the RP only region. Figure 13 shows these results with $h_{RP} = 1$ (left) and $h_{RP} = 4$ (right).

**Summary of Basic Linear Models**

Compared to a similar model without behavioural change, this basic model is characterized by a greater range of parameters that enables all three species to persist, even though in most of the additional region, the system becomes a three species food chain. This is similar to findings by Krivan (2000) who showed that a non-adaptive system has a more restricted parameter space allowing 3-species coexistence than an adaptive one. Also, the expansion of the three species region due to predator behaviour comes mostly at the expense of previously resource-consumer region and only a relatively small amount from the resource-predator region. This is similar to the findings by Krivan and Diehl (2005). However, unlike their model, the model presented here does not require that the consumers be more profitable than the basal resource. This is a result of how prey choice was modelled in the present work and in Krivan and Diehl (2005). They modelled the prey choice of the predator according to the “diet rule” where the predator never drops the more profitable food item from its diet while I modelled the predator’s behaviour assuming a trade-off between the two consumption rates (similar to Krivan 2000). However, in agreement with Krivan and Diehl (2005), as the consumers become less profitable relative to the resource, the size of the three species region decreases. The resource-predator region increases in size while the upper bound of predator existence drops, thus reducing the overall size of the three species region. However, the size of the omnivory region within the 3-species region increased from 11% of the three species
parameter space for the case where consumers are more profitable to 76% for the case where the resource is slightly more profitable. This is caused by the reduction of the total 3-species region while the size of the omnivorous region increases slightly as the ratio of consumer to resource profitability goes down. Thus, when the consumer has a higher profitability than the basal resource, three species coexistence is more likely, but omnivory is relatively rare compared to three species food chains. When consumer profitability is equal to or lower than resource profitability, three species coexistence is restricted to a smaller parameter space, but omnivory is relatively common within the set of 3-species systems.

The next sections contain modifications to the basic model. Their analysis was based mainly on numerical integration.

4. Basic model with slower rate of trait change and linear predator trade-off (n=1)

Slow adaptive change was explored to see whether the predicted parameters yielding omnivory would differ if species adapted to food and risk via evolution rather than behaviour. For this model, I lowered the value of the rate of trait change ($v_P$ and $v_C$) from 10 to 0.1. This value is low enough that the rate of change is slow relative to the population dynamics, but high enough that the trait values would still be sensitive to the changes in population. To compensate for the slower rate of behaviour change, the runtime for the model has been increased to 100,000 time steps and the value of $\epsilon$ is decreased from the $10^{-6}$ in the standard model to $10^{-10}$. These compensations were required because the speed of adaptive change affected the time it took for the system to settle to its final state and the type of final state reached depended on the interaction between the predator’s response speed and
its sampling/mutational bias when traits approached their extreme values. The rest of the parameters used are identical to those in the previous section, where the consumers are more profitable than the resource.

The result of this set of simulations was very similar to the behavioural model with its faster trait response rate. The size and position of the coexistence regions matches closely with the previous model. However, the slower rate of trait change tends to destabilize the three species system as the portion of parameter space exhibiting non-equilibrium dynamics in the food chain region has increased in size (figure 14). This is a largely a consequence of the stabilizing effect of the predator's diet choice.

5. A linear predator preference trade-off (n=1); Models with minimum consumption rates

For this model I examined the effects of imposing a minimum predation rate of the predator on both the consumer and the resource. This model simulates a system where the predator cannot avoid consuming both types of prey item while foraging. This means that, if all species persist, there will be omnivory, even if the predator’s preference is completely for one of the prey items. It is a reasonable change to make in the model because most predators are capable of catching the occasional individual of prey that they are not particularly well-adapted for exploiting. The modifications to the equations are:

\[ S_{RP}(u)\lambda_{RP} \rightarrow S_{RP}(u)(\lambda_{RP} - \lambda_{Rmin}) + \lambda_{Rmin} \]  \hspace{1cm} (7a)

\[ S_{CP}(u)\lambda_{CP}(w) \rightarrow S_{CP}(u)(\lambda_{CP}(w) - \lambda_{Cmin}) + \lambda_{Cmin} \]  \hspace{1cm} (7b)
\( \lambda_{R \text{min}} \) is the minimum capture rate for the resource by the predator, while \( \lambda_{C \text{min}} \) is the minimum capture rate for the consumer. I begin by modelling the effects of \( \lambda_{R \text{min}} \) and \( \lambda_{C \text{min}} \) separately, and then examine their combined effects. For the simulation of this model, I only used the parameter set where consumers are more profitable.

5a. A linear predator preference trade-off (n=1); Minimum consumption only applies to consumers

For this model, I examine the case where \( \lambda_{R \text{min}} \) is kept at 0, while \( \lambda_{C \text{min}} \) varies between 0.001, 0.005 and 0.01. These are one-tenth, one-half and the full value of the minimum possible value of \( \lambda_{C \text{TP}}(w) \). These values were chosen so that the difference between \( \lambda_{C \text{TP}}(w) \) and \( \lambda_{C \text{min}} \) would not result in a negative value. The results are shown in Figure 15. The results from \( \lambda_{C \text{min}} = 0.001 \) are identical to the case without minimum consumption (section 3a), indicating that \( \lambda_{C \text{min}} = 0.001 \) is low enough not to have a significant impact on the model. For \( \lambda_{C \text{min}} = 0.005 \) and \( \lambda_{C \text{min}} = 0.01 \), the three species region is reduced to about 50% of the total parameter space and the omnivory region has decreased in size to only 3% of the total parameter space. These results are due to the predator being unable to switch away from the consumer even at low consumer density, thus preventing their recovery.

5b. A linear predator preference trade-off (n=1); Minimum consumption only applies to basal resources

To examine the importance of minimum resource consumption, I simulated a model where the minimum consumer capture rate (\( \lambda_{C \text{min}} \)) is zero, while the value of the minimum resource capture rate (\( \lambda_{R \text{min}} \)) is varied between 0.005, 0.01, and 0.05, which are respectively one-
The results of all three simulations are very similar to the results of the basic model (section 3a) where there are no minimum consumption rates. There is a minor reduction in the size of the three species coexistence region as $\lambda_{R_{\text{min}}}$ increased. The region went from 53.5% of the total parameter space at $\lambda_{R_{\text{min}}} = 0.005$ to 48% at $\lambda_{R_{\text{min}}} = 0.05$. This is mostly due to the reduction of region of total consumer preference at high predator mortalities.

These results seem to indicate that a low value of minimum resource consumption rate causes a minor reduction in the size of the three species coexistence area. However, the predator would always be considered omnivorous in a model with minimum consumption rates, even if the predator completely prefers the consumer. Thus, it is possible for a predator to be an omnivore for a large range of parameter values by maintaining a very low minimum capture rate for the resource.

5c. A linear predator preference trade-off ($n=1$); Minimum consumption applies to both consumers and basal resources

In this model, I imposed a minimum consumption rate on both the consumer and resource ($\lambda_{C_{\text{min}}} = 0.005$ and $\lambda_{R_{\text{min}}} = 0.05$). The results of this set of simulations (figure 17) appear to be a simple combination of the results from the two previous sections (figure 15 and 16). The minimum consumer consumption rate affects the bottom portion of the parameter space by increasing the RP only region while the minimum resource consumption influenced only the top portion by increasing the RC only region. These results indicate that (1) restricting the predator’s ability to switch away from a prey item reduces its ability to persist and (2) the
effects of predator-consumer interaction and predator-resource interaction are independent of each other.

6a. Basic model with non-linear predator tradeoff (n=0.5); Consumer is more profitable to the predator than is the resource

To investigate the effects of non-linear tradeoff functions for predator preference, I consider the case where the tradeoff curve is convex (n=0.5) and where a generalist should be favoured. The simulations were run using the standard parameters where the consumer is more profitable than the resource, and results are shown in figure 18.

Compared to the linear model, the result for the non-linear model with a convex tradeoff curve (figure 18, top left) showed a pronounced increase in the size of the omnivorous region, especially where productivity and predator mortality are low. The entire region consists only of equilibrium dynamics and the region has also been shifted upwards by an increase in the size of the resource-predator region. Compared to the basic model, the top section of the graph where the system acts as a three species food chain remains unchanged. The total three species area is 50% of the total parameter space, slightly smaller compared to the 54% in the linear (n=1) case. Of the three species area, 80% functions as a three species food chain while the other 20% is omnivorous. In terms of absolute area, three species food chain takes up about 40% of the total parameter space while the omnivory region takes up a little less than 10%. A graph of the predator preference (u) is shown on figure 19. The transition from food chain to omnivory is more gradual compared to the linear case (figure 20).
While the omnivory region is larger than in the linear tradeoff case, the size of the region is still less than expected. For a convex tradeoff, one would expect the optimal u value to always produce an intermediate result. One of the reasons this may not be true is because the preference tradeoff functions (equations 3a, 3b) are embedded within Hollings’ Type II functional and this may have reduced the effects of non-linear tradeoff. Another possibility may be because the consumer is so much more profitable that it still overcomes the effect of the non-linear tradeoff for the majority of the parameter space. When the profitabilities are equal (see below), a non-linear trade-off produces a much greater fraction of omnivorous systems within the parameter space where all three species persist.

6b. Basic model with non-linear predator tradeoff (n=0.5); Consumer and resource are equally profitable to the predator

The non-linear model with a convex predator tradeoff was then analyzed using the parameter set where both the consumers and basal resource are equally profitable. With both of its food sources equally profitable, the prediction was that the predator should become an omnivore. The result of the numerical integration of this model (figure 18, top right) showed a substantial increase in the size of the resource-predator region when compared to its counterpart with a linear tradeoff (figure 18, top left). As in the non-linear model with the standard ‘consumer more profitable’ parameters, the shape of the curve where the three species region borders the resource-consumer region remains unchanged compared to the linear case (figure 10), although the composition of the three species region has changed from food chain to omnivory. The size of the three species area has shrunk to 18.5% of the
total parameter space. However, the three species food chain region is not present in this model. The omnivorous region makes up 85% of the three species area. The remaining 15% consists of a small region of stable three species competition that is found between the RP only and the three species omnivory regions. This competition region was present as well in the linear case. The omnivory region takes up 15.8% of the total parameter space while the competition region takes up 2.7%.

6c. Basic model with non-linear predator tradeoff (n=0.5); Basal resource more profitable to the predator

This non-linear model was also explored with the parameter set where basal resource is more profitable to the predator. The graph of the results (fig. 18, bottom left) showed a large resource-predator region and a large resource-consumer region with no three species region between them. The resource-predator region has grown in size so much that the three species region has been eliminated and consumers can only exist in the parameter space where the predator mortality is so high that the predator cannot survive on the basal resource alone. This three species area is only about 1.5% of the total parameter space. Because of the convex trade-off curve, even a predator whose primary preference is for the basal resource can incorporate the less profitable consumers into its diet without reducing its fitness very much. Thus, even low densities of consumers can be targeted by the predator and are unable to reinvade a system where predator population is high. The only exception is when productivity is high. At high productivity and moderately high predator mortality, where predators are still viable, there is a small region of non-equilibrium competition and within this region is a very small three species omnivory region. These regions are the result of
cyclic dynamics that enabled all three species to coexist. In this region the predator and the resource undergo large cycles that allowed the consumer to persist at very low densities even in the presence of the predator. However, this type of dynamics is highly sensitive to the parameters, especially the handling time of consumers on resource. It is probably not biologically significant.

**Summary of Basic Model with Convex Predator Trade-off**

Compared with the linear model, the non-linear model with convex predator trade-off is more likely to exhibit omnivory. In the non-linear models where the consumers were more profitable and where the consumers and resources were equally profitable, there was a much larger omnivory region than in their linear counterparts. This is expected since convex trade-off curves tend to favour generalists. However, this increase in omnivory is due to food chain dynamics being converted into omnivory dynamics rather than expansions of omnivory into resource-predator or resource-consumer regions. In actuality, the non-linear trade-off in predator preference has caused the entire three species region to be reduced in size due to increases in the resource-predator region, leading to an almost complete disappearance of three species region in the model where the resource is more profitable.

These results are similar to the ones from the model with a minimum consumption rate. In both models, the predator cannot or does not completely drop the consumer from its diet, either because it is unable to do so in the previous model or because selection does not favor such a restriction in this model. In both cases, the inability of the predator to avoid consuming the consumers even when the consumer population are at low levels reduces the
consumer’s ability to persist in the system and thus decreases the size of the region where all three species can coexist. However, this inability of the predator to completely avoid either prey also allows a higher proportion of the three species region to give rise to omnivory.

**Dimorphic Model**

For modelling a system with a concave predator trade-off, the previous model, which represented omnivory as a predator behavioural trait, is not applicable. With a concave trade-off curve, predators would naturally tend to become specialized on either the basal resource or the consumer. In order to portray a predator that is able to switch between these two specialist modes of feeding, a dimorphic model is required. The equations describing the model are:

\[
R' = R\left[ r \left( 1 - \frac{R}{K} \right) - \frac{\lambda_{RC}(w)C}{1 + h_{RC}\lambda_{RC}(w)R} - \frac{\lambda_{RP}P_R}{1 + h_{RP}\lambda_{RP}R} \right] 
\]  

(7a)

\[
C' = C\left[ \frac{\lambda_{CP}(w)P_c}{1 + h_{CP}\lambda_{CP}(w)C} - m_c \right] 
\]  

(7b)

\[
P'_R = P_R\left[ \frac{\lambda_{RP}P_R}{1 + h_{RP}s_{RP}(u)\lambda_{RP}R} - m_p \right]
\]

\[
- P_R\sigma \left( \frac{\lambda_{CP}(w)C}{1 + h_{CP}\lambda_{CP}(w)C} - \frac{\lambda_{RP}P_R}{1 + h_{RP}s_{RP}(u)\lambda_{RP}R} \right)
\]

\[
+ P_C\sigma \left( \frac{\lambda_{RP}P_R}{1 + h_{RP}s_{RP}(u)\lambda_{RP}R} - \frac{\lambda_{CP}(w)C}{1 + h_{CP}\lambda_{CP}(w)C} \right) 
\]  

(7c)

\[
P'_C = P_C\left[ \frac{\lambda_{CP}(w)C}{1 + h_{CP}\lambda_{CP}(w)C} - m_p \right]
\]

\[
- P_C\sigma \left( \frac{\lambda_{RP}P_R}{1 + h_{RP}s_{RP}(u)\lambda_{RP}R} - \frac{\lambda_{CP}(w)C}{1 + h_{CP}\lambda_{CP}(w)C} \right)
\]

\[
+ P_R\sigma \left( \frac{\lambda_{RP}P_R}{1 + h_{RP}s_{RP}(u)\lambda_{RP}R} - \frac{\lambda_{CP}(w)C}{1 + h_{CP}\lambda_{CP}(w)C} \right) 
\]  

(7d)
PR and PC represent predator morphs that specialize on the basal resource and the consumer respectively. The function \( \sigma(\Delta) \) describes rate at which a predator switches from one feeding mode to the other mode as a function of the difference between the intake rate of the two food items. Here I followed Abrams and Matsuda (2004), and used an exponential function for \( \sigma(\Delta) \) such that:

\[
\sigma(\Delta) = Z \exp(V\Delta)
\]

(8)

where \( Z \) is the transition rate when \( \Delta \) is zero, thus representing the predator’s sampling behaviour. The parameter \( V \) is a positive constant that determines the sensitivity of the transition function to the difference in food intake rate. The function \( \sigma(\Delta) \) is always greater than zero and is an increasing function of \( \Delta \). In this dimorphic model, the consumer retains the ability to alter its activity level \( (w) \). The equation controlling this behvioural response is similar to the one in the monomorphic model as shown in (2b).

Because of the way the dimorphic model is constructed, omnivory must be redefined. In the monomorphic model, omnivory can be defined at an individual level where each individual predator is able to adopt a range of omnivorous behaviour as a feeding strategy. In the dimorphic model, each individual predator adopts a feeding mode focusing on either the basal resource or the consumer. In this model, omnivory can only be defined on a population level where an omnivorous population is one that contains both types of morphs in significant proportions. For this model, the level of omnivory \( (u) \) is defined to be the proportion of consumer-focused morphs over the entire predator population. The outcomes of the simulations are classified to be three species food chain if \( u>0.99 \), three species competition if \( u<0.01 \) and three species omnivory if \( u \) is between those two values.
The dimorphic model approximates the monomorphic model best when the values for both the sampling rate (Z) and the sensitivity (V) are low. The values for the sampling rate (Z) and the sensitivity (V) were 0.000001 and 30 respectively. Increasing the sampling rate can greatly increase the size of the omnivorous region.

The model was simulated with the parameter set used in the basic model with the consumers more profitable (section 3a). The result of this model is shown in figure 21. Compared with the monomorphic model in section 3a, the three species coexistence region is smaller at 50% of the total parameter space. This is mainly due to the reduction in the omnivorous region (3% of the total parameter space in this model) due to the increase in RP only region. The three species food chain region is maintained at 47% of the parameter space, similar to the monomorphic model with linear trade-off. A major difference between the dimorphic and monomorphic model is the increase in the size of regions that exhibit non-equilibrium dynamics.

**Discussion**

Is omnivory a rare phenomenon in nature? Some recent empirical studies have shown omnivorous interactions to be ubiquitous (Coll and Guershon 2002; Arim and Marquet 2004; Thompson et al. 2007) while others have claimed that omnivory is not as ecologically important as suggested (Williams and Martinez 2004). The relative frequency of omnivory also differs between different communities, with omnivory being more common in marine systems than in terrestrial or stream and lake systems (Shurin et al. 2006; Thompson et al.
2007). However, theoretical studies have indicated that omnivory should be uncommon in nature (Pimm and Lawton 1978; Pimm 1982). The addition of omnivorous links destabilizes the system (Pimm and Lawton 1978; Pimm 1982) and causes the middle species to become vulnerable to exclusion (Holt and Polis 1997; Diehl and Feissel 2000; Mylius et al. 2001). Adaptive foraging theory also suggests that omnivory should be rare. Denno and Fagan (2003) pointed out that nutritional quality increases with trophic level while biomass decreases. Since a predator should focus on the more profitable prey item, it should prefer the more valuable consumer and ignore the less valuable resource, thus creating a food chain. Krivan and Diehl (2005) incorporated this idea explicitly with their “diet rule” in the formulation of their model. Even though no such explicit rule was present in the models presented in this thesis, the results clearly showed a tendency towards the formation of a food chain as opposed to omnivory in several cases. These were cases where it was advantageous for the top species to concentrate all of its foraging on the more valuable, middle level species.

The cases presented in the previous section do not cover all the possible ranges of omnivory models, but from those cases, we can still derive some interesting conclusions: (1) Adaptive behaviour in the predator facilitates three species coexistence while adaptive behaviour in consumers appears to stabilize the system. (2) There are two different types of omnivorous strategies. In the first type, which I call strong omnivory, the top predator consumes both of its prey items in fixed proportions when the system is at equilibrium, and consumes substantial amounts of both prey at all times when there are population cycles. In the second type, which I call weak omnivory, the predator concentrates on one prey item most of the
time and switches to temporarily incorporate the other prey only when that prey’s population
is high. (3) The configuration of a three species system depends on whether the conditions
allow either the consumer or the predator to invade when rare. If both the consumer and the
predator can invade a system consisting of the other species along with the basal resource,
then the system will be omnivorous. If the condition of the system is such that the predator
can invade a system of resource and consumers but cannot exist solely on the resource alone,
then the system will become a three species food chain, unless large population cycling leads
to a weak omnivory dynamic. (4) Contrary to Krivan and Diehl (2005), the middle consumer
need not be more profitable than the basal resource to the top predator to observe omnivory.
Alternating the profitability of consumer to predator and the profitability of resource to predator
produces independent effects. (5) A low level of minimum consumption by the predator on
the resource will not have a significant impact on the size of the three species coexistence
region. This allows the predator to be considered omnivorous over a wide range of
parameter values. (6) Factors that prevent or discourage the predator from completely
specializing on one prey item will tend to increase the size of the omnivory region, but will
also decrease the overall size of the three species coexistence region.

The addition of adaptive predator preference has a large impact on the system. By allowing
the predator to adjust its preference, the region of three species coexistence is greatly
enlarged. These findings corroborate with earlier findings (Krivan 2000; Krivan and Diehl
2005) that an adaptive predator is more likely to allow the persistence of all three species,
especially under the condition where consumer profitability is high while resource
profitability is low. However, analysis of the present set of models shows that under such
conditions, most of the region of three species coexistence would consist of the predator focusing solely on the highly profitable consumer while ignoring the basal resource. Thus, most of the systems would be 3-species food chains rather than omnivorous.

Previous theoretical findings by Uchida and Drossel (2007) seem to indicate that the addition of predator avoidance behaviour tends not to have a significant impact on food web stability. On the other hand, Amarasekare (2007) showed that a temporal refuge for the consumer can promote coexistence. The results of the models examined here indicate that allowing the consumer to optimize its activity level in response to the population changes in predators and basal resource can increase the instability of the system if it is the only adaptive mechanism present. However, when both the predator and the consumer are able to alter their behaviour, the ability of the consumer to adaptively vary its activity level has a significant stabilizing effect on the system. It thus appears that interactions between multiple species that are all able to alter their behaviour in response to other species can create unexpected effects that are still poorly understood at this time.

Two types of omnivory are predicted from the results. One type involves consumption of both prey items at intermediate proportions. While the proportion may fluctuate over time, the predator always consumes nontrivial amounts of both prey items. I refer to this type as strong omnivory. Examples of this type are relatively common in the literature (Buck et al. 2003; Lancaster et al. 2005; Mooney and Tillberg 2005; Camus, Daroch and Opazo 2008). The second type of omnivory occurs when the predator preys predominantly on one prey item, but rapidly switches to include the other item when the relative abundance of that
second item exceeds a certain level. Omnivory of this kind appeared most prominently when only the predator was allowed to adapt and the populations of the three species exhibited large cycles. I call this type of dynamics weak omnivory. Red squirrels preying on the spruce bark beetle after beetle outbreaks had reduced seed cone availability (Pretzlaw et al. 2006) may be an example of this type of omnivory. Strong omnivory requires that both the predator and consumer are able to exist solely on the basal resource and are also able to invade the system when rare. This is quite different from weak omnivory, which is mainly driven by population cycling.

Contrary to Krivan and Diehl 2005, the condition that the consumer be more profitable than the resource is not required for either three species coexistence or omnivory. Even when the consumer is as profitable as the resource, there is a large increase in the area of three species coexistence when the predator exhibits adaptive behaviour. Furthermore, a larger percentage of the three species region exhibits omnivory dynamics compared to the case when the consumer is more profitable. The difference between these findings and those in the previous study by Krivan and Diehl (2005) are the results of different tradeoffs in the predator's foraging. Krivan and Diehl assumed that both potential foods of the top species were encountered simultaneously at fixed rates, and that only the decision to accept the poorer quality food could be altered. Here, the top species cannot forage at maximal rates for both prey simultaneously, and the relative capture rates of the two are changed adaptively.

The greater proportion of parameter space exhibiting omnivory is partly due to the greater proportion of 3-species systems that were omnivorous in this study compared to Krivan and
Diehl (2005). Comparing the analytical results in figure 1 with the numerical results of figure 8 shows that the region where the predator can invade only if the consumer exists (region C in figure 1) corresponds fairly closely to the three species food chain region in figure 8; while the omnivory region in figure 8 corresponds to the region where both predators and consumers exist by themselves with the basal resource and can invade a system containing only the other two (region D in figure 1). Some differences exist primarily because the invasion boundaries in figure 1 assume stable equilibria, which is not always the case. In any case, the approximate correspondence means that the size of the three species region is determined by the predator invasion curve, which is the threshold for predator invasion into a system of resource and consumers (curve 5e), and the consumer invasion curve, which represents the threshold for consumer invasion into a resource-predator only system (curve 5j). The relative proportion of omnivory within the three species region is determined by the predator existence curve, which is the boundary for the predator to be able to sustain itself solely on the resource (curve 5f).

The profitabilites of the consumer and the resource to the predator have independent effects on the three curves. Consumer profitability only affects the predator invasion curve. An increase in consumer profitability raises the curve and increases the size of the three species region by reducing the RC only region, but this only increases the region with three species food chain since the predator existence curve has not changed. Conversely, altering the profitability of the resource to the predator only affects the predator existence curve and the consumer invasion curve. An increase in resource profitability raises both of the curves and leads to a reduction in the overall size of the three species region by enlarging the RP only
region. However, since the two curves do not rise at the same rate, it is possible for the omnivory region to increase in size even as the three species region is reduced. Thus, because the size of the regions do not depend explicitly on the ratio of the two profitabilities, the condition that consumer be more profitable is not required for omnivory. However, if the profitability of the basal resource becomes too high, the predator existence curve would overtake the predator invasion curve and eliminate the three species existence region. Thus, the region of omnivory should be greatest in size when the profitability of the consumer and resource is similar.

If we assume that organisms of similar physiological structure should have profitabilities that are more similar than those with different physiology, then a consequence of the previous finding is the prediction that an omnivorous system should be relatively more common when both of the prey items (the consumer and the resource) are physiologically similar. Otherwise, if the two prey items are very different, then a food chain system would be more likely to develop. Thus, omnivory involving two prey items that are taxonomically similar should be more common than omnivory in which the two prey are more distantly related. This leads to the secondary prediction that a system involving herbivores and producers that exhibits omnivory should be less common than food chain interactions in such a system. Omnivory should be relatively more common than simple food chains at higher trophic levels where the nutritional values of foods at different levels are likely to differ less than plants and animals. This prediction seems to be in agreement with Thompson et al. (2007) which finds that while the trophic position of plants and herbivores are well defined in food webs, omnivorous interaction are very common at higher trophic levels.
Results from the model with an imposed minimum consumption rate shows that adding a permanent weak omnivorous link only slightly reduced the size of the three species coexistence region. This indicates that omnivory can be common when the predator only consumes a very low amount of the resource. This seems to corroborate with findings by McCann et al. (1998) that weak predator-resource interactions do not inhibit three species coexistence. Another finding from this model is that imposing a minimum consumer consumption rate or a minimum resource consumption rate also produces independent effects. A minimum consumer capture rate reduces the consumer’s ability to invade when rare and thus increases the size of the RP only region. The effect on the three species coexistence is similar to when resource profitability is increased. Imposing a minimum resource capture rate has the opposite effect of reducing the predator’s ability to sustain itself at high predator mortality; this is similar to the effect of reducing the consumer’s profitability.

These results show a consistent trend where factors that promote omnivory dynamics (consumer and resource having similar profitabilities; the presence of minimum consumption rates; convex tradeoffs) also tend to reduce three species coexistence. This is in agreement with older theoretical work which suggests that omnivory reduces food web viability (Pimm and Lawton 1978; Pimm and Rice 1987).

One of the limitations of the models presented here is the interchangeability of the consumer and the resource as a food source for the predator. I have not considered the case where the two prey provide different nutritional or other non-additive benefits. Coll and Guershon
(2002) pointed out that feeding on multiple prey items can provide complementary effects and can greatly enhance fitness. Denno and Fagan (2003) similarly indicated that arthropod predators, which are frequently nitrogen-limited, can increase their nitrogen uptake by including other nitrogen-rich predators in its diet. Bjorndal (1991) found that the yellow-bellied slider turtle (*Trachemys scripta scripta*) can greatly increase its digestive efficiency by choosing an omnivorous diet.

Another limitation of this analysis is the simplicity of the food web in the model. A three species community was used in all the cases. More complex food webs that include more species, contain additional links, or spanned more trophic levels may produce different results. Namba et al. (2008) showed that the addition of a new species to a simple intraguild predation food web can either stabilize or destabilize the system depending on the position of the new species. Many empirical studies have indicated that omnivorous species are often embedded in complicated food webs with many connections (Arim and Marquet 2004; Thompson et al. 2007) and thus it is important to investigate omnivory in a broader context where the species involved have alternative prey (Holt and Huxel 2007). It may be as McCann et al. (1998) have suggested that these links consist primarily of weak interactions.

Many of the examples of omnivorous systems in literature involve either arthropods (Coll and Guershon 2002) or benthic communities where detritus is the basal resource (Polis and Strong 1996; Tavares-Cromar and Williams 1996; HilleRisLambers et al. 2006). These are often donor controlled systems where feeding on the basal resource has little to no impact on its growth rate. Pimm (1982) argued that omnivory can be extensive if the population growth
rate of a prey species is not effected by those feeding on it. This was based on his theory that omnivory was rare in other systems because dynamic instability caused extinction in one or more species. This idea now seems unlikely. Kendall et al. (1998) found that roughly 30% of long-term population records exhibited cycles. Nevertheless, the apparent correlation of omnivory with systems that are likely to have stable dynamics is intriguing.

HilleRisLambers et al. (2006) examined a donor controlled system and found that omnivorous interactions were present even in highly productive environments. These donor controlled systems have similar properties to a stage-structured population in that the growth rate of certain segments of the prey population is not affected by the predator. Previous work has shown that stage-structured populations can allow for greater stability at high productivity (Abrams and Quince 2005) and models by Pimm and Rice (1987) have shown that omnivory has a much smaller impact on stability in a population that contains a life history structure. Modifying the models presented in this thesis to investigate a donor controlled system or a system with structured population would be worthwhile. However, the fact that the equilibrium-based invasion analysis and the numerical simulations suggested similar parameter ranges characterized by omnivory suggests that donor-controlled resource dynamics might not change the results significantly.

The addition of adaptive foraging behaviours in omnivorous food web models facilitates three species coexistence; however, by allowing the predator to select its prey, there is a strong tendency for the predator to consume only the more profitable species and ignore the less profitable one. This creates three species food chains and restricts omnivory. This
problem of increasing omnivory at the expense of reducing coexistence remains to be resolved in future studies.
Table 1: Definition of the parameters used in the models

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>Carrying capacity of resources</td>
</tr>
<tr>
<td>r</td>
<td>Intrinsic growth rate of resources</td>
</tr>
<tr>
<td>$\lambda_{RC_{\text{max}}}$</td>
<td>Maximum capture rate of consumers on resources</td>
</tr>
<tr>
<td>$\lambda_{CP_{\text{max}}}$</td>
<td>Maximum capture rate of predators on consumers</td>
</tr>
<tr>
<td>$\lambda_{RC_{\text{min}}}$</td>
<td>Minimum capture rate of consumers on resources</td>
</tr>
<tr>
<td>$\lambda_{CP_{\text{min}}}$</td>
<td>Minimum capture rate of predators on consumers</td>
</tr>
<tr>
<td>$\lambda_{RP}$</td>
<td>Capture rate of predators on resources</td>
</tr>
<tr>
<td>$h_{RC}$</td>
<td>Time spent by consumers handling a resource</td>
</tr>
<tr>
<td>$h_{CP}$</td>
<td>Time spent by predators handling a consumer</td>
</tr>
<tr>
<td>$h_{RP}$</td>
<td>Time spent by predators handling a resource</td>
</tr>
<tr>
<td>$e_{RC}$</td>
<td>Conversion efficiency of resources into consumers</td>
</tr>
<tr>
<td>$e_{CP}$</td>
<td>Conversion efficiency of consumers into predators</td>
</tr>
<tr>
<td>$e_{RP}$</td>
<td>Conversion efficiency of resources into predators</td>
</tr>
<tr>
<td>$m_C$</td>
<td>Density independent mortality rate of consumers</td>
</tr>
<tr>
<td>$m_P$</td>
<td>Density independent mortality rate of predators</td>
</tr>
<tr>
<td>$v_P$</td>
<td>Predator trait change rate</td>
</tr>
<tr>
<td>$v_C$</td>
<td>Consumer trait change rate</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Sampling bias</td>
</tr>
<tr>
<td>n</td>
<td>Curvature of trade-off in predator preference</td>
</tr>
<tr>
<td>a</td>
<td>Curvature of function relating consumers activity level to predation risk</td>
</tr>
<tr>
<td>b</td>
<td>Curvature of function relating consumers activity level to foraging ability</td>
</tr>
<tr>
<td>$\lambda_{R_{\text{min}}}$ (minimum consumption model)</td>
<td>Minimum imposed capture rate of predators on resource</td>
</tr>
<tr>
<td>$\lambda_{C_{\text{min}}}$ (minimum consumption model)</td>
<td>Minimum imposed capture rate of predators on consumers</td>
</tr>
<tr>
<td>Z (dimorphic model)</td>
<td>Sampling rate</td>
</tr>
<tr>
<td>V (dimorphic model)</td>
<td>Sensitivity</td>
</tr>
</tbody>
</table>
**Table 2:** The standard values for model parameters and initial conditions used in simulations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Standard Value</th>
<th>Initial Conditions</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r$</td>
<td>1</td>
<td>$R(0)$</td>
<td>$K$</td>
</tr>
<tr>
<td>$\lambda_{RC_{max}}$</td>
<td>0.2</td>
<td>$C(0)$</td>
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</tr>
<tr>
<td>$\lambda_{CP_{max}}$</td>
<td>0.11</td>
<td>$P(0)$</td>
<td>1.0</td>
</tr>
<tr>
<td>$\lambda_{RC_{min}}$</td>
<td>0</td>
<td>$u(0)$</td>
<td>0.5</td>
</tr>
<tr>
<td>$\lambda_{CP_{min}}$</td>
<td>0.01</td>
<td>$w(0)$</td>
<td>0.4</td>
</tr>
<tr>
<td>$\lambda_{RP}$</td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h_{RC}$</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$e_{RC}$</td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$m_{C}$</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$v_{P}$</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$v_{C}$</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>0.000001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$n$</td>
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<tr>
<td>$a$</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$b$</td>
<td>2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the model with linear predator trade-off (n=1) under three assumptions about the presence of adaptive behaviour.

<table>
<thead>
<tr>
<th></th>
<th>No adaptive behaviour</th>
<th>Consumer with adaptive behaviour</th>
<th>Predator with adaptive behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h_{CP}$</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>$h_{RP}$</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>$e_{CP}$</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>$e_{RP}$</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td><strong>R</strong> only</td>
<td>5.7</td>
<td>5.6</td>
<td>5.7</td>
</tr>
<tr>
<td><strong>RC</strong> only</td>
<td>58.5</td>
<td>59.5</td>
<td>35.3</td>
</tr>
<tr>
<td><strong>RCP</strong> (chain)</td>
<td>-</td>
<td>-</td>
<td>37.7</td>
</tr>
<tr>
<td><strong>RCP</strong> (omni)</td>
<td>24.5</td>
<td>24.2</td>
<td>12.4</td>
</tr>
<tr>
<td><strong>RCP</strong> (comp)</td>
<td>-</td>
<td>-</td>
<td>0.4</td>
</tr>
<tr>
<td><strong>RP</strong> only</td>
<td>11.3</td>
<td>10.7</td>
<td>8.7</td>
</tr>
</tbody>
</table>
Table 4: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the basic model with linear predator trade-off (n=1) where both consumers and predator exhibited adaptive behaviour. Three different profitabilities were examined.

<table>
<thead>
<tr>
<th></th>
<th>Consumers more profitable (Model 3a)</th>
<th>Equal profitability (Model 3b)</th>
<th>Resource more profitable (Model 3c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>h\textsubscript{CP}</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>h\textsubscript{RP}</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>e\textsubscript{CP}</td>
<td>0.2</td>
<td>0.2</td>
<td>0.15</td>
</tr>
<tr>
<td>e\textsubscript{RP}</td>
<td>0.05</td>
<td>0.1</td>
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<tr>
<td>R only</td>
<td>5.4</td>
<td>5</td>
<td>4.4</td>
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<tr>
<td>RC only</td>
<td>32.6</td>
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<td>55.8</td>
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<td>RCP (chain)</td>
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<td>RCP (omni)</td>
<td>6</td>
<td>8.5</td>
<td>7.3</td>
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<td>RCP (comp)</td>
<td>0.4</td>
<td>2.5</td>
<td>1.5</td>
</tr>
<tr>
<td>RP only</td>
<td>7.7</td>
<td>18.3</td>
<td>30.1</td>
</tr>
</tbody>
</table>
Table 5: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the basic model with linear predator trade-off (n=1) and consumers more profitable. The table illustrates the effects of different handling times.

<table>
<thead>
<tr>
<th>Models with consumers more profitable, various handling times</th>
<th>h&lt;sub&gt;CP&lt;/sub&gt;</th>
<th>h&lt;sub&gt;Rp&lt;/sub&gt;</th>
<th>e&lt;sub&gt;CP&lt;/sub&gt;</th>
<th>e&lt;sub&gt;Rp&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>h&lt;sub&gt;CP&lt;/sub&gt;</td>
<td>0.5</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>h&lt;sub&gt;Rp&lt;/sub&gt;</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>e&lt;sub&gt;CP&lt;/sub&gt;</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>e&lt;sub&gt;Rp&lt;/sub&gt;</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>R only</td>
<td>5.4</td>
<td>5.4</td>
<td>5.4</td>
<td>5.5</td>
</tr>
<tr>
<td>RC only</td>
<td>18.6</td>
<td>49</td>
<td>32.5</td>
<td>32.7</td>
</tr>
<tr>
<td>RCP (chain)</td>
<td>61.9</td>
<td>31.5</td>
<td>43.3</td>
<td>52.9</td>
</tr>
<tr>
<td>RCP (omni)</td>
<td>6</td>
<td>5.9</td>
<td>8.4</td>
<td>3.6</td>
</tr>
<tr>
<td>RCP (comp)</td>
<td>0.4</td>
<td>0.4</td>
<td>1.3</td>
<td>0.1</td>
</tr>
<tr>
<td>RP only</td>
<td>7.7</td>
<td>7.7</td>
<td>9.1</td>
<td>5.2</td>
</tr>
</tbody>
</table>
Table 6: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the basic model with linear predator trade-off (n=1). Rate of trait change ($v_P$ and $v_C$) are lowered to 0.1 and $\varepsilon$ is reduced to $10^{-10}$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h_{CP}$</td>
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</tr>
<tr>
<td>$h_{RP}$</td>
<td>2</td>
</tr>
<tr>
<td>$e_{CP}$</td>
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</tr>
<tr>
<td>$e_{RP}$</td>
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</tr>
<tr>
<td>$v_P$</td>
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</tr>
<tr>
<td>$v_C$</td>
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<tr>
<td>$\varepsilon$</td>
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<table>
<thead>
<tr>
<th>Type</th>
<th>Percentage</th>
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</thead>
<tbody>
<tr>
<td>R only</td>
<td>5.9</td>
</tr>
<tr>
<td>RC only</td>
<td>32.1</td>
</tr>
<tr>
<td>RCP (chain)</td>
<td>47.9</td>
</tr>
<tr>
<td>RCP (omni)</td>
<td>5.6</td>
</tr>
<tr>
<td>RCP (comp)</td>
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<tr>
<td>RP only</td>
<td>7.7</td>
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</table>
Table 7: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the models with minimum consumption rates applied only to one prey.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum consumption rate only applied to consumers</th>
<th>Minimum consumption rate only applied to resource</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h_{CP}$</td>
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<td>1</td>
</tr>
<tr>
<td>$h_{RP}$</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>$e_{CP}$</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>$e_{RP}$</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>$\lambda_{Rmin}$</td>
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<td>0</td>
</tr>
<tr>
<td>$\lambda_{Cmin}$</td>
<td>0.001</td>
<td>0.005</td>
</tr>
<tr>
<td>R only</td>
<td>5.4</td>
<td>5.4</td>
</tr>
<tr>
<td>RC only</td>
<td>32.6</td>
<td>32.6</td>
</tr>
<tr>
<td>RCP (chain)</td>
<td>47.6</td>
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<tr>
<td>RCP (omni)</td>
<td>5.3</td>
<td>3.1</td>
</tr>
<tr>
<td>RCP (comp)</td>
<td>0.5</td>
<td>0.3</td>
</tr>
<tr>
<td>RP only</td>
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<td>12.1</td>
</tr>
<tr>
<td>R only</td>
<td>5.4</td>
<td>5.4</td>
</tr>
<tr>
<td>RC only</td>
<td>33.3</td>
<td>34.1</td>
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<td>RCP (omni)</td>
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<td>6.1</td>
</tr>
<tr>
<td>RCP (comp)</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>RP only</td>
<td>7.7</td>
<td>7.7</td>
</tr>
</tbody>
</table>
Table 8: Parameter values and results (percentage of total parameter space) from the models with minimum consumption rates applied to both prey

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum consumption rate applies to both consumers and resource</td>
<td></td>
</tr>
<tr>
<td>$h_{CP}$</td>
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</tr>
<tr>
<td>$h_{RP}$</td>
<td>2</td>
</tr>
<tr>
<td>$e_{CP}$</td>
<td>0.2</td>
</tr>
<tr>
<td>$e_{RP}$</td>
<td>0.05</td>
</tr>
<tr>
<td>$\lambda_{Rmin}$</td>
<td>0.05</td>
</tr>
<tr>
<td>$\lambda_{Cmin}$</td>
<td>0.005</td>
</tr>
<tr>
<td>R only</td>
<td>5.4</td>
</tr>
<tr>
<td>RC only</td>
<td>38.7</td>
</tr>
<tr>
<td>RCP (chain)</td>
<td>40.3</td>
</tr>
<tr>
<td>RCP (omni)</td>
<td>3.1</td>
</tr>
<tr>
<td>RCP (comp)</td>
<td>0.2</td>
</tr>
<tr>
<td>RP only</td>
<td>12.2</td>
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</table>
Table 9: Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the basic model with non-linear predator trade-off (n=0.5) using three different profitabilities

<table>
<thead>
<tr>
<th></th>
<th>Consumers more profitable (Model 6a)</th>
<th>Equal profitability (Model 6b)</th>
<th>Resource more profitable (Model 6c)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>h\textsubscript{CP}</strong></td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>h\textsubscript{RP}</strong></td>
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<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>e\textsubscript{CP}</strong></td>
<td>0.2</td>
<td>0.2</td>
<td>0.15</td>
</tr>
<tr>
<td><strong>e\textsubscript{RP}</strong></td>
<td>0.05</td>
<td>0.1</td>
<td>0.2</td>
</tr>
<tr>
<td><strong>R only</strong></td>
<td>5.4</td>
<td>5</td>
<td>4.4</td>
</tr>
<tr>
<td><strong>RC only</strong></td>
<td>32.8</td>
<td>47.2</td>
<td>51</td>
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<tr>
<td><strong>RCP (chain)</strong></td>
<td>40.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>RCP (omni)</strong></td>
<td>9.6</td>
<td>15.8</td>
<td>0.1</td>
</tr>
<tr>
<td><strong>RCP (comp)</strong></td>
<td>0.4</td>
<td>2.7</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>RP only</strong></td>
<td>11.3</td>
<td>29.3</td>
<td>43.2</td>
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**Table 10:** Parameter values and results (percentage of total parameter space exhibiting different types of communities) from the dimorphic model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Dimorphic Model</th>
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<td>$h_{CP}$</td>
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<tr>
<td>$h_{RP}$</td>
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</tr>
<tr>
<td>$e_{CP}$</td>
<td>0.2</td>
</tr>
<tr>
<td>$e_{RP}$</td>
<td>0.05</td>
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<tr>
<td>$Z$</td>
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</tr>
<tr>
<td>$V$</td>
<td>30</td>
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<tr>
<td>R only</td>
<td>5.5</td>
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<tr>
<td>RC only</td>
<td>31.9</td>
</tr>
<tr>
<td>RCP (chain)</td>
<td>47</td>
</tr>
<tr>
<td>RCP (omni)</td>
<td>32</td>
</tr>
<tr>
<td>RCP (comp)</td>
<td>0.1</td>
</tr>
<tr>
<td>RP only</td>
<td>12.3</td>
</tr>
</tbody>
</table>
Figure 1: Analysis of species invasion on the productivity-predator mortality (K-m_p) parameter space. Region A contains only the basal resource. Region B contains both the resource and the consumer. Region C is where predators can invade a system of resource and consumers but cannot exist if the consumers are absent. In region D, both the consumers and predators can exist by themselves with the basal resource and both consumers and predators can successfully invade a system containing only the other two. In region E, only the basal resource and the predators are present, consumers are unable to invade. Behavioural parameters are u=1, w=1 for predator invasion, and u=0, w=1 for consumer invasion. The other parameters are: r=1, λ_max=0.2, λ_min=0, λ_RP=0.1, λ_Cmax=0.11, λ_Cmin=0.01, h_RC=1, h_RP=2, h_CP=1, e_RC=0.1, e_RP=0.05, e_CP=0.2, m_C=0.03.
Figure 2a: The value of $u$ during predator invasion is reduced to 0.5, leading to a much smaller region C.

Figure 2b: The value of $u$ during consumer invasion is 0.05. The consumer invasion threshold is no longer a horizontal line but a rising curve that reduces the area of region D.
Figure 3: The effects of consumer behavior on dynamics. The left hand side assumes $w = 1$ (no consumer behavior) while the right hand side assumes adaptive adjustment of $w$. The other parameters are: $r=1$, $\lambda_{RP}=0.1$, $\lambda_{RCmax}=0.2$, $\lambda_{RCmin}=0$, $\lambda_{CPmax}=0.11$, $\lambda_{CPmin}=0.01$, $h_{RC}=1$, $h_{RP}=2$, $h_{CP}=1$, $c_{RC}=0.1$, $c_{RP}=0.05$, $c_{CP}=0.2$, $m_{c}=0.03$, $a=2$, $b=2$, $\varepsilon = 0.000001$, $v_{C}=10$, $u=0.5$, $n=1$. The purple region is resource only, the grey region has both resource and consumer, the blue region contains all three species, and the red region contains the resource and predators. The regions with lighter color denote sustained fluctuations in densities.

Figure 4: This is a 3d graph of the values of $w$ for the model with adaptive consumer behaviour. The vertical axis is $w$ and the horizontal axis are $K$ and $m_{p}$. The top represents $w$ values near 1, a fully active consumer, while bottom represents $w$ values near 0, where the consumer is completely inactive or not present.
**Figure 5:** The results of the model where only predators can change its behaviour. The purple region is resource only; the dark grey region is RC-only at equilibrium; the light grey is RC at non-equilibrium dynamics; the dark green region is three species food chain at equilibrium while the light green region is non-equilibrium dynamics; the dark blue is the omnivory region at equilibrium while the light blue is at non-equilibrium; the red region has the resource and the predator at equilibrium while the pink region is non-equilibrium. The parameters are: $r=1$, $\lambda_{RP}=0.1$, $\lambda_{RC_{max}}=0.2$, $\lambda_{RC_{min}}=0$, $\lambda_{CP_{max}}=0.11$, $\lambda_{CP_{min}}=0.01$, $h_{RC}=1$, $h_{RP}=2$, $h_{CP}=1$, $e_{RC}=0.1$, $e_{RP}=0.05$, $e_{CP}=0.2$, $m_c=0.03$, $\varepsilon=0.000001$, $\nu_p=10$, $w=1$, $n=1$.

**Figure 6:** The top figures are simulations of population over time (solid line represents the resource; short dash line is consumer; long dash line is predator). The bottom figures represent the predator preference ($u$) over the same time period. The left figures are from the region with strong omnivory ($K=16$, $m_p=0.018$) while the right are from the weak omnivory region ($K=16$, $m_p=0.04$).
Figure 7: This is a graph of the value of $u$ for the model where only predators can change its behaviour. The vertical axis is $u$ while the two horizontal axis are $K$ and $m_P$. The top of the graph represents $u$ values near 1 where the predator preference is completely for the consumer and the system is a food chain. The bottom represents either a complete preference for the basal resource due to consumer absence, or the absence of the predator at high predator mortalities. For most values of $K$, the value of $u$ drops quickly from near 1 to near 0 over a narrow range of $m_P$, representing a sharp transition from the three species food chain region to the RP only region through a small omnivory region.
Figure 8: Simulation result of the basic model with linear predator trade-off (n=1) and where the consumer is more profitable than the resource. The color scheme is identical to the one used in figure 5. The parameters are: $r=1$, $\lambda_{RP}=0.1$, $\lambda_{RCmax}=0.2$, $\lambda_{RCmin}=0$, $\lambda_{CPmax}=0.11$, $\lambda_{CPmin}=0.01$, $h_{RC}=1$, $h_{RP}=2$, $h_{CP}=1$, $e_{RC}=0.1$, $e_{RP}=0.05$, $e_{CP}=0.2$, $m_{C}=0.03$, $a=2$, $b=2$, $\varepsilon=0.000001$, $v_{C}=10$, $v_{P}=10$.

Figure 9: Simulation results of the basic model. The left figure represents predator preference ($u$) as a function of $K$ and $m_{P}$ while the right figure represents consumer activity. The values of $u$ and $w$ shown here are the averaged final values.
Figure 10: Simulation result of the basic model with linear predator trade-off (n=1) and where the consumer and the resource are equally profitable. The color code is identical to the one used in the previous figure. One main difference in this figure is the large size of the “competition” region which is colored yellow. Another is the appearance of a “weak” omnivory region within the unstable portion of the three species food chain region. The parameters in this model is similar to the ones used in figure 8 except: $e_{RP}=0.1$, $e_{CP}=0.2$, $h_{RP}=1$, $h_{CP}=2$.

Figure 11: Simulation result of the basic model with linear predator trade-off (n=1) and where the resource is more profitable than the consumer. The color codes are the same as the one used in previous figures. The parameters in this model is similar to the ones used in figure 8 except: $e_{RP}=0.2$, $e_{CP}=0.15$, $h_{RP}=2$, $h_{CP}=2$. 
Figure 12: Results from the simulations with alternate $h_{CP}$ values. For the left figure, $h_{CP} = 0.5$, half of the original value, while the right figure has $h_{CP} = 2$, twice the original value. The rest of the parameters are identical to the ones used in figure 8. Changing the predator-consumer handling time greatly changes curvature of the boundary between the RC only region and the three species food chain region. A lower handling time allows for predator existence at much higher predator mortalities. However, it has no effect on the omnivorous or RP only regions.

Figure 13: Results from the simulations using alternate $h_{RP}$ values. For the left figure, $h_{RP} = 1$, one-half of the original value, while the right figure has $h_{RP} = 4$, double of the original value. The rest of the parameters are identical to the ones used in figure 8. The results from these graphs show that altering the predator-resource handling time only affects the bottom portion of the graph which contains the omnivory and RP only regions. There is little effect on the boundary between the food chain region and the RC only region.
Figure 14: The left graph is the result of the model with normal response speed ($v_P$ and $v_C = 10$) while the right graph is the model with a slow response speed ($v_P$ and $v_C = 0.1$). The slower response speed reduces stability in a three species system and increases the size of the non-equilibrium area in the three species food chain region. The value of $\varepsilon$ is decreased from $10^{-6}$ in the standard model to $10^{-10}$ in this model. The other parameters are identical to the ones used in figure 8.
Figure 15: The results of the model with a minimum consumer capture rate. The values of $\lambda_{C_{\text{min}}}$ used in this model are 0.001, 0.005, and 0.01, which are respectively one-tenth, one-half and the full value of the minimum value of $\lambda_{CP}(w)$. The top left graph is ($\lambda_{C_{\text{min}}} = 0.001$), the top right is ($\lambda_{C_{\text{min}}} = 0.005$) and the bottom graph is ($\lambda_{C_{\text{min}}} = 0.01$). The rest of the parameters used are identical to the ones used in figure 8 where consumers are more profitable. The grey regions are consumer only. The red and pink regions are RP only, with the pink section representing non-equilibrium systems. Both the green and blue regions are regions where all three species coexist. In the green region, the system is a 3-species food chain while in the blue region the system is omnivorous. For all these regions, the lighter color represents the non-equilibrium systems. For the case with $\lambda_{R_{\text{min}}} = 0.001$, the result is very similar to basic model without any minimum capture rates (figure 8).
Figure 16: These are the results of keeping the minimum predator on consumer capture rate ($\lambda_{C_{min}}$) at zero while setting the minimum predator on resource capture rate ($\lambda_{R_{min}}$) at 0.005, 0.01, and 0.05 respectively. All of the results are similar to the basic model without any minimum capture rates (figure 8) but there is a reduction in the 3-species region as $\lambda_{R_{min}}$ increases.

*Note that since the predator is maintaining a minimum resource consumption rate, the predator would be considered omnivorous over any of the regions (green and blue) where all three species coexist. However, in the green region, predator preference is completely for the consumer ($u > 0.99$) while in the blue region predator preference is intermediate ($0.01 > u > 0.99$).
Figure 17: These are the results of including both minimum consumption rates. The values of the minimum rates are $\lambda_{C_{\text{min}}} = 0.005$ and $\lambda_{R_{\text{min}}} = 0.05$. The result resembles a simple combination of the results depicted in figure 15 and 16.

*Note that since the predator is maintaining a minimum consumption rate on both prey, the predator would be considered omnivorous over any of the regions (green and blue) where all three species coexist. However, in the green region, predator preference is completely for the consumer ($u > 0.99$) while in the blue region predator preference is intermediate ($0.01 > u > 0.99$).
Figure 18: The results of the model with non-linear predator trade-offs ($n=0.5$). The top left graph is from the simulation where consumers are more profitable, the top right is where consumers and resource are equally profitable, and the bottom left is where the resource is more profitable. The color scheme is similar to the ones used in previous figures.
Figure 19: The results of the predator preference (u) from the model with non-linear predator trade-offs (n=0.5) where consumers are more profitable. The transition from three species food chain dynamics (top of the plateau) to omnivory dynamics (the side) is less abrupt compared to the linear trade-off case (figure 9). The results shown here are averaged final values.

Figure 20: A cross-section of the values of u at K=6. The left figure is where the trade-off is linear, the left figure is where the trade-off is non-linear (n=0.5). The right portion of the graphs where u is 0 is where high predator mortality has eliminated the predators.
Figure 21: The results of the dimorphic model with sampling rate \( Z = 0.000001 \) and the sensitivity \( V = 30 \). The rest of the parameters are identical to the ones used in the basic model with consumers more profitable as described in figure 8. The left figure is a graph of the different regions and the right figure depicts the relative abundance of the consumer-focused morphs over the same parameter space.
Literature Cited


Case, T.J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society **42**: 239-266.


