Appendix 1

Predator–prey models with density dependence and handling time were first explored in the context of inverted biomass pyramids (IBPs) in Wang et al. (2009). Here, we re-derive their results using predator–prey isoclines. The isocline approach provides mechanistic insights and a clear means for visualizing IBPs and the associated stability of the predator–prey dynamics.

Density dependence:
To analyze the effect of density-dependence on biomass pyramid structure, we assume predators have a type I functional response, \( f(N) = aN \). In a type I system prey consumption by predators increases linearly with prey biomass. Here, \( a \) represents attack rate or encounter probability of predators on prey. We envision a system similar to IBPs observed in pelagic planktonic communities where filter feeders have no handling time for prey.

Analysis of a predator–prey system with type I functional response reveals the effects of density dependence on IBP systems. The zero-growth isoclines are:

\[
\text{Predator isocline:} \quad N = \frac{d}{ca} \tag{1}
\]

\[
\text{Prey isocline:} \quad P = \frac{r}{a} \left(1 - \frac{N}{K}\right) \tag{2}
\]

with equilibrium points \((N^*, P^*) = \left(\frac{d}{ca}, \frac{r}{a} \left(1 - \frac{d}{caK}\right)\right)\). The IBP criterion \( P^*/N^* > 1 \) is:

\[
P^*/N^* = \frac{r}{a} \left(\frac{c}{d} - \frac{1}{aK}\right) > 1 \tag{3}
\]
Figure A1. The effect of prey carrying capacity and predator encounter rate on IBP structure. (A) Predator-prey isoclines without density dependence (light colors) and (B) with density dependence (dark colors). The prey isocline is blue; predator isocline, red. Adding density dependence decreases the chance of an IBP as prey growth rate is decreased. The parameters are $r = 0.13, K = 100, d = 0.1, c = 1, a = 8/300$. State-space regions below the 45° dashed line represent Eltonian biomass pyramids, while those above the 45° line are IBPs.

Wang et al. (2009) found that increasing prey growth rate ($r$), conversion efficiency ($c$), favors IBP structure by increasing the prey isocline (blue) and lowering the predator isocline respectively. We can verify this analytically. Let $R$ be the ratio between predator and prey biomass $R = P^*/N^*$. With respect to growth rate ($r$), $\frac{\partial R}{\partial r} = \frac{c}{d} - \frac{1}{ak}$ while the effect of conversion efficiency is $\frac{\partial R}{\partial c} = \frac{r}{d}$. Because all parameters are positive, $\frac{c}{d} \geq \frac{1}{ak}$ for there to be a positive biomass ratio, i.e. positive biomass for predator and prey. This means that $\frac{\partial R}{\partial r} > 0$ and $\frac{\partial R}{\partial c} > 0$ and therefore increase the predator–prey biomass ratio. They also found that decreasing the predator death rate ($d$) favors IBP structure by shifting the predator isocline to the left. Analytically, $\frac{\partial R}{\partial d} = -\frac{rc}{d^2} < 0$ which means increasing $d$ leads to a smaller ratio (decreasing $d$ leads to a higher ratio). Finally, predator per capita predation rate ($a$) and carrying capacity ($K$) can both favor IBP structure with conditions ($rc > d$). As long as prey biomass decreases faster than predator biomass, high per capita predation rates will favor IBP, otherwise increases in predation rate will only serve to decrease isoclines and disfavor IBP (Fig. 1). In the case of carrying capacity ($K$), as it gets larger and tends towards infinity, the prey isocline becomes increasingly horizontal, intra-prey competition declines, and as $K$ goes to infinity the model converges on a density-independent Lotka–Volterra predator–prey model and increases the likelihood of an IBP. $\frac{\partial R}{\partial K} = \frac{r}{ak^2} > 0$ and $\frac{\partial R}{\partial a} = \frac{r}{a^2k} > 0$. 

2
Our conclusions differ slightly from Wang et al. (2009) because of differences in our approach and a different definition of what favors an IBP. We explicitly examine the equilibrial ratio of predator to prey biomass, \( \frac{P^*}{N^*} \). We also found conversion efficiency \( c \) works slightly differently from Wang et al. (2009) because we are working in biomass units and conversion efficiency can be no larger than 1.

**Handling time**
We demonstrate the effect of handling time on IBP structure by adding handling time, \( h \), to the predator’s functional response resulting in a type II functional response \( f(N) = \frac{aN}{1 + ahN} \). While handling prey, additional prey cannot be captured. The type II functional response would be observed in IBP systems similar to coral reefs with primary and secondary consumers, where piscivore predators differ in their encounter rates and handling times on evasive prey. With handling time, prey experience safety in numbers via a dilution effect.

With handling time, the isoclines become:

Predator isocline:

\[
N = \frac{d}{a(c - dh)}
\]  

(4)

Prey isocline:

\[
P = \frac{r}{a} \left(1 + ahN\right) \left(1 - \frac{N}{K}\right)
\]  

(5)

with the equilibrium point being \( (N^*, P^*) = \left(\frac{d}{a(c - dh)}, \frac{r}{a} \left(1 + \frac{dh}{c - dh}\right) \left(1 - \frac{d}{aK(c - dh)}\right)\right) \) and the IBP criterion being:

\[
\frac{P^*}{N^*} = rc \left(\frac{1}{a} - \frac{1}{aK(c - dh)}\right) > 1
\]  

(6)
Figure A2. The effect of handling time on the structure of IBPs. The color of the isoclines and parameters are as before with only death rate changed to $d = 0.04$. Darker colors indicate regions of increased handling time ($h$) with $h = (0, 0.425, 0.85, 1.275, 1.7, 2.125)$. The combination dotted and dashed black line traces changes in the equilibrium point due to increasing handling time. One sees that handling time works for IBP structure among prey by creating an Allee effect among prey, but also works against IBP structure as the predator isocline increases. Overall, handling time hinders IBP structure.

Here we provide the analytical details of our results pertaining to vigilance. We model fixed and facultative vigilance first assessing when the costs of vigilance impact the prey’s growth rate, and then assessing when the costs impact the prey’s maximum carrying capacities.

*Fixed vigilance*

**Tradeoffs between safety and growth rate:**

We obtain the zero growth isoclines by setting our predator and prey growth equations to zero and rearranging for $N$ and $P$. 


Predator isocline:

\[ N = \frac{d(k + bu)}{cm} \]  

(7)

Prey isocline:

\[ P = r(1 - u)\left(\frac{k + bu}{m}\right)\left(1 - \frac{N}{K}\right) \]  

(8)

We then obtain equilibrium predator and prey population sizes \((N^*, P^*)\) respectively: \((N^*, P^*) = \left(\frac{d(k + bu)}{cm}, r(1 - u)\left(\frac{k + bu}{m}\right)\left(1 - \frac{d(k + bu)}{cm}\right)\right)\). These equilibria are used to assess trophic structure using the predator-prey biomass ratio \(R = \frac{P^*}{N^*} = r(1 - u)\left(\frac{c}{d} - \frac{k + bu}{mK}\right)\). The effects of the parameters on the predator–prey biomass ratio is much the same, aside from the addition of vigilance \((u)\) such that \(\frac{\partial R}{\partial r} = (1 - u)\left(\frac{c}{d} - \frac{k + bu}{mK}\right) > 0, \frac{\partial R}{\partial d} = -\frac{re(1 - u)}{d^2} < 0, \frac{\partial R}{\partial c} = \frac{r(1 - u)}{d} > 0, \frac{\partial R}{\partial K} = \frac{r(1 - u)(k + bu)}{mk^2} > 0, \) and \(\frac{\partial R}{\partial m} = \frac{r(1 - u)(k + bu)}{m^2k} > 0\). For predator lethality \(\frac{1}{k}\), we can replace it with a variable \(g\) which means the predator–prey biomass ratio is \(R = \frac{P^*}{N^*} = r(1 - u)\left(\frac{c}{d} - \frac{bu}{mK} - \frac{1}{gmK}\right)\). Taking the partial, we get \(\frac{\partial R}{\partial g} = \frac{r(1 - u)}{g^2mK} > 0\), increasing predator lethality increases the predator–prey biomass ratio. Looking at effectiveness of vigilance \((b)\), we get \(\frac{\partial R}{\partial b} = -\frac{ru(1 - u)}{mk} < 0\) and as such increasing \(b\) always decreases the predator–prey biomass ratio. Looking at vigilance itself, we see that it always decreases the predator–prey biomass ratio. The partial is \(\frac{\partial R}{\partial u} = -r\left(\frac{c}{d} - \frac{k + bu}{mK}\right) - \frac{rb}{mk}(1 - u)\) which is always negative. The above results hold for \(u < 1\) (which means \(\frac{P^*}{N^*} = 0\), and for all other situations where \(\frac{P^*}{N^*} > 0\).

**Tradeoffs between safety and carrying capacity**

We obtain the zero growth isoclines for predators and prey, now with the costs of vigilance impacting the maximum carrying capacity.

Predator isocline:

\[ N^* = \frac{d(k + bu)}{cm} \]  

(9)

Prey isocline:

\[ P^* = \frac{r}{m}(k + bu)\left(1 - u - \frac{d(k + bu)}{Kcm}\right) \]  

(10)

The effects of the various parameters have much the same effect on the predator prey isoclines and biomass ratio at equilibrium as previously modeled. We note that the predator-prey biomass ratio at equilibrium now becomes zero at lower levels of vigilance then when modeled with the tradeoff on growth rate. Now, the biomass ratio becomes zero when \((1 - u) < \left(\frac{d(k + bu)}{Kcm}\right)\). We obtain this condition by setting the biomass ratio, \(P^*/N^*\)(from line 251 in the main text), equal to zero and rearranging the equation.
Facultative vigilance

Tradeoffs between safety and growth rate

When the tradeoff is between safety and growth-rate and is facultative, optimal vigilance is

$$u^* = \sqrt{\frac{mP}{rb(1-N/K)}} - \frac{k}{b}.$$  

For there to be a non-complex solution to optimal vigilance, prey populations must always be less than carrying capacity $N < K$; this constraint follows in the rest of the analysis.

Increasing predator biomass ($P$) and encounter rate ($m$) both have the same effect of increasing optimal vigilance, 

$$\frac{\partial u^*_r}{\partial P} = \frac{1}{2} \sqrt{\frac{m}{rb(1-N/K)}}$$

and

$$\frac{\partial u^*_r}{\partial m} = \frac{1}{2} \sqrt{\frac{P}{rbm(1-N/K)}},$$

as they are both always positive. For prey growth rate ($r$), we get

$$\frac{\partial u^*_r}{\partial r} = -\frac{1}{2} \sqrt{\frac{mP}{r^3b(1-N/K)}}$$

decreasing optimal vigilance as it increases.

Replacing predator lethality $\frac{1}{k}$ with $g$, optimal vigilance becomes 

$$u^*_r = \sqrt{\frac{mP}{rb(1-N/K)}} - \frac{1}{gb}.$$  

Taking the partial derivative with respect to $g$, we get

$$\frac{\partial u^*_r}{\partial g} = \frac{1}{bg^2}$$

which is always positive meaning increased predator lethality leads to increased optimal vigilance. Increasing prey population ($N$) always increases optimal vigilance also as

$$\frac{\partial u^*_r}{\partial N} = \frac{1}{2k} \sqrt{\frac{mP}{rb(1-N/K)}}.$$

Increasing carrying capacity ($K$) decreases optimal vigilance as

$$\frac{\partial u^*_r}{\partial K} = -\frac{N}{2k^2} \sqrt{\frac{mP}{rb(1-N/K)}}$$

which is negative. The effectiveness of vigilance offers a more interesting result. Its partial derivative is

$$\frac{\partial u^*_r}{\partial b} = \frac{k}{b^2} - \frac{1}{2} \sqrt{\frac{mP}{rb^2(1-N/K)}} = 2k - \frac{\sqrt{\frac{mbP}{r(1-N/K)}}}{2b^2}.$$  

At $b = 0$, the partial derivative is positive and increasing the effectiveness of vigilance increase optimal vigilance; however, this reaches a maximum

$$b = \frac{4rk^2(1-N/K)}{mP}$$

beyond which increasing the effectiveness of vigilance ($b$) decreases optimal vigilance. Now vigilance is modeled as a dynamic game, where predator and prey biomasses affect vigilance behavior, and vigilance levels affect predator and prey biomasses. We obtain the predator and prey isoclines similarly to our fixed vigilance models:

Prey isocline:

$$P = \frac{r}{4mb}(k + b)^2 \left(1 - \frac{N}{K}\right)$$  \hspace{1cm} (11)

Predator isocline:

$$P = \frac{rm}{b} \left(\frac{c}{d}\right)^2 N^2 \left(1 - \frac{N}{K}\right)$$  \hspace{1cm} (12)

The equilibrium being: \((N^*, P^*) = \left(\frac{d(k+b)}{2mc}, \frac{r}{4mb}(k + b)^2 \left(1 - \frac{d(k+b)}{2mcK}\right)\right)\).
We can see how the parameters effect the predator–prey biomass ratio \( R = \frac{P^*}{N^*} = \frac{r}{2b} \left( k + b \right) \left( \frac{c}{d} \frac{k + b}{2mK} \right) \). The effects of prey growth rate \((r)\), predator death rate \((d)\), conversion efficiency \((c)\), carrying capacity \((K)\), and encounter rate \((m)\) remain effectively the same \( \frac{\partial R}{\partial r} = \frac{k + b}{2b} \left( \frac{c}{d} \frac{r}{d} \partial c \frac{r}{d} \partial K = \frac{r(k + b)^2}{mK^2} \right), \text{and} \frac{\partial R}{\partial m} = \frac{r(k + b)^2}{m^2K^2} \). Doing the same replacement of \( \frac{1}{k} \) with \( g \), we get \( \frac{\partial R}{\partial g} = \frac{r}{2g^2b} \left( \left( \frac{1}{g} \frac{k + b}{mK} - \frac{c}{d} \right) \right) \). This differs from previous examples in that it starts positive before turning negative. This means that increasing predator lethality initially increases the predator–prey biomass ratio before decreasing it. Looking at effectiveness of vigilance \((b)\), we find that \( \frac{\partial R}{\partial b} = -\frac{r(b^2d + k(2cmK - dk))}{4b^2dmK} \). Consequently, \( \frac{\partial R}{\partial b} \) is always less than 0 as the inequality \( 2cmK - dk > 0 \) must be satisfied (rearranging the inequality, we get \( \frac{c}{d} \frac{k}{2mK} > \frac{c}{d} \frac{k + b}{2mK} \) the latter equation a necessary condition of positive predator–prey biomass ratio).

**Tradeoffs between safety and carrying capacity**

Optimal vigilance when the tradeoff is between safety and carrying capacity is \( u^* = \frac{mP}{rb} \). Increasing predator biomass \((P)\) and encounter rate \((m)\) both have the same effect of increasing optimal vigilance, \( \frac{\partial u^*}{\partial P} = \frac{1}{2} \sqrt{\frac{m}{rbP}} \) and \( \frac{\partial u^*}{\partial m} = \frac{1}{2} \sqrt{\frac{P}{rbm}} \) as they are both always positive. With prey growth rate \((r)\), we get \( \frac{\partial u^*}{\partial r} = -\frac{1}{2} \sqrt{\frac{mP}{r^2b}} \) decreasing optimal vigilance as it increases. Once again replacing predator lethality \((1)\) with \( g \), we get \( \frac{\partial u^*}{\partial g} = \frac{1}{bg^2} \) identical to the tradeoff between safety and growth rate. Effectiveness of vigilance also has a similar effect as before with \( \frac{\partial u^*}{\partial b} = \frac{k}{b^2} \).

\[
\frac{1}{2} \sqrt{\frac{mP}{rb^3}} = \frac{2k - \sqrt{\frac{mbP}{r} \frac{r}{2b^2}}}{2b^2}, \text{ initially increasing optimal vigilance until reaching a maximum} \left( b = \frac{4k^2r}{mP} \right) \text{ then decreasing it.}
\]

Including optimal vigilance into the predator–prey system with costs impacting the prey’s maximum carrying capacity results in the following prey and predator isoclines:

**Prey isocline:**

\[
P = \frac{rb}{4m} \left( 1 + \frac{k}{b} - \frac{N}{K} \right)^2 \quad (13)
\]

**Predator isocline:**

\[
P = \frac{rm}{b} \left( \frac{cN}{d} \right)^2 \quad (9)
\]
If the prey’s optimal vigilance is between 0 and 1, we find the following stable equilibria for prey,

\[ N^* = \frac{Kd(k+b)}{2Kcm+bd}, \]

and predators,

\[ P^* = \frac{rm}{b} \left( \frac{Kc(b+k)}{2Kcm+bd} \right)^2 \]

with a predator–prey biomass ratio is

\[ R = \frac{P^*}{N^*} = \frac{rmKc^2(b+k)}{bd(2Kcm+bd)}. \]

Once again, we can assess the effect of each parameter. For prey growth rate \( (r) \), we have \( \frac{\partial R}{\partial r} = \frac{Kmc^2}{bd(2Kcm+bd)} > 0 \), and for carrying capacity \( (K) \) and encounter rate \( (m) \), we get \( \frac{\partial R}{\partial K} = \frac{rmc^2(b+k)}{(2Kcm+bd)^2} > 0 \) and \( \frac{\partial R}{\partial m} = \frac{rKc^2(b+k)}{(2Kcm+bd)^2} > 0 \). For conversion efficiency \( (c) \), we get \( \frac{\partial R}{\partial c} = \frac{2cKmr(b+k)(bd+Kcm)}{bd(bd+2Kcm)^2} > 0 \). These are always positive meaning increasing them always increases the predator–prey biomass ratio. For death rate, we get \( \frac{\partial R}{\partial d} = - \frac{2c^2Kmr(b+k)(bd+Kcm)}{bd^2(bd+2Kcm)^2} < 0 \); for effectiveness of vigilance \( (b) \), we get \( \frac{\partial R}{\partial b} = - \frac{c^2Kmr(b^2d+2Kcmk+2bdk)}{b^2d(bd+2Kcm)^2} < 0 \); and for predator lethality \( \left( \frac{1}{k} \right) \), we do the same substitution with \( g \) and get \( \frac{\partial R}{\partial g} = - \frac{c^2Kmr}{g^2bd(bd+2Kcm)} < 0 \). All of these are always negative meaning that increasing them decrease the predator–prey biomass ratio.

**Optimization methodology**

We confirmed the validity of our optimal vigilance levels for both facultative vigilance models by taking the second derivatives of the prey per biomass growth rate equations and confirming that they represent a local maximum (with a negative second derivative). We obtain the same result for both models: \( -(2b^2mNP)/(bu + k)^3 \).

**Stability analysis**

We can use linear stability analysis to derive the stability of our predator–prey system at equilibrium. Deriving the Jacobian matrix generally leads to extremely long eigenvalues. Such eigenvalues can be solved for, but analyzing the Jacobian qualitatively by looking at the slopes of the isoclines at the equilibrium point is simpler and easier especially when vigilance is assumed to operate on a fast, behavioral dynamic such that it is always at equilibrium with respect to population dynamics. For example, if we analyze the general Rosenzweig–MacArthur model with a type II functional response, we see that the Jacobian matrix

\[ J = \begin{bmatrix} + & -1 \\ + & 0 \end{bmatrix} \]

when the prey population at equilibrium is less than the maximum of the isocline. At such an equilibrium, the trace of the Jacobian is always positive \( \text{Tr}(J) > 0 \) as is the determinant \( \text{Det}(J) > 0 \). Because of this, at least one eigenvalue will always be positive, meaning the system will always be asymptotically unstable. We can use the same principles to derive the stability of our systems.
We used Jacobian matrix and determinant analysis to assess each model’s equilibrium for stability. We first assessed the Rosenzweig–MacArthur predator prey model with fixed vigilance regardless of tradeoffs. Qualitatively, the Jacobian matrix at the equilibrium point is:

\[ J = \begin{bmatrix} p & -q \\ 0 & 0 \end{bmatrix}. \]

We assess the trace and determinate for stability with respect to the slopes of the predator–prey isoclines at the intercept and find the trace is negative and the determinant is positive. Therefore, the fixed vigilance model is stable at equilibrium.

Next, we assess the Rosenzweig–MacArcher predator–prey model with facultative vigilance and tradeoffs felt on prey growth rate when the equilibrium is within the IBP state space (Fig. 2A–B). Qualitatively, the Jacobian matrix at the equilibrium point is:

\[ J = \begin{bmatrix} p & -q \\ 0 & 0 \end{bmatrix}. \]

Once again, the trace is negative and the determinant is positive. Therefore, we conclude the facultative vigilance model when the equilibrium is an IBP is also stable. This stability analysis can also be applied to the equilibrium for our facultative vigilance model with tradeoffs impacting carrying capacity as it has the same qualitative Jacobian across all equilibria such that \(0 < u’ < 1\).

Finally, we assess the Rosenzweig–MacArthur predator–prey model with facultative vigilance and tradeoffs felt on prey growth rate when the equilibrium is within the Eltonian state space (Fig. 2C–D). The Jacobian matrix is different because now the equilibrium intersects at a negative slope of the predator isocline yielding:

\[ J = \begin{bmatrix} p & -q \\ 0 & 0 \end{bmatrix}. \]

The trace is always positive; however, the determinant is indeterminate. This Jacobian is similar to a strictly competitive model, and as such, the determinant is positive only when the product of the intraspecific effects are greater than the product of the interspecific effects. Therefore, we conclude that if this condition is met, the facultative vigilance model equilibrium in Eltonian state–space can be stable.