

Peter A. Abrams and Michael H. Cortez. 2015. The many potential indirect interactions between predators that share competing prey. Ecological Monographs VOL: pp-pp.

Appendix C Effects of perturbations to predator mortality rates for unequal predator conversion efficiencies

Differentiating the N_1 and N_2 terms of P_4 with respect to d_1 and d_2 yields four equations that describe how small, controlled changes in the mortality rate of one species alter the equilibrium densities of the two predators:

$$\frac{\partial N_2^*}{\partial d_1} = \frac{1}{\Delta\Delta} [b_{21}c_{21}(c_{11}k_2 - c_{12}k_1\alpha q) + b_{22}c_{22}(c_{12}k_1 - c_{11}k_2\alpha/q)] \quad (\text{C1})$$

$$\frac{\partial N_1^*}{\partial d_2} = \frac{1}{\Delta\Delta} [b_{12}c_{12}(c_{22}k_1 - c_{21}k_2\alpha q) + b_{11}c_{11}(c_{21}k_2 - c_{22}k_1\alpha/q)] \quad (\text{C2})$$

$$\frac{\partial N_1^*}{\partial d_1} = \frac{-1}{\Delta\Delta} [b_{21}c_{21}(c_{21}k_2 - c_{22}k_1\alpha q) + b_{22}c_{22}(c_{22}k_1 - c_{21}k_2\alpha/q)] \quad (\text{C3})$$

$$\frac{\partial N_2^*}{\partial d_2} = \frac{-1}{\Delta\Delta} [b_{11}c_{11}(c_{11}k_2 - c_{12}k_1\alpha q) + b_{12}c_{12}(c_{12}k_1 - c_{11}k_2\alpha/q)]. \quad (\text{C4})$$

Each derivative can be positive or negative. All sign combinations are possible except for the case where all of the derivatives are positive; see theorem 1 below. Positive signs for equations (C3) and (C4) imply that the respective species exhibits the hydra effect. Note that because of the Lotka-Volterra form of our model, the right hand sides of the above equations do not depend on d_1 or d_2 .

The following subsections address the classification methods based on (i) the effects of mortality perturbations on the equilibrium density of heterospecifics and (ii) those effects corrected for the effect on the perturbed species. The last subsection addresses the effects of increases in non-selective mortality rates.

Theorem 1. *Regions where $\partial N_j^*/\partial d_k > 0$ for all j, k cannot arise in system (1).*

Proof. For presentational purposes, in this proof we will use the notation α_{ij} to denote the interspecific prey competition coefficients. Recall that $\alpha_{12} = \alpha q$ and $\alpha_{21} = \alpha/q$.

Choose any parameter set. Let $\{\alpha_{12}, F_{\partial N_j^*/\partial d_k}(\alpha_{12})\}$ denote the set of points where $\partial N_j^*/\partial d_k = 0$. The functions $F_{\partial N_j^*/\partial d_k}(\alpha_{12})$ are defined by equations (C1) through (C4). They are linear in α_{12} . We make use of the differences

$$F_{\partial N_1^*/\partial d_1}(\alpha_{12}) - F_{\partial N_2^*/\partial d_1}(\alpha_{12}) = \frac{k_1 \Delta}{b_{22}c_{22}c_{11}c_{21}k_2} (b_{22}c_{22} - \alpha_{12}b_{21}c_{21}) \quad (\text{C5})$$

$$F_{\partial N_2^*/\partial d_2}(\alpha_{12}) - F_{\partial N_1^*/\partial d_2}(\alpha_{12}) = \frac{k_1 \Delta}{b_{12}c_{12}c_{11}c_{21}k_2} (\alpha_{12}b_{11}c_{11} - b_{12}c_{12}). \quad (\text{C6})$$

Assume $\Delta > 0$ and $\bar{\Delta} > 0$. For sufficiently small α_{ij} , we have that $\partial N_1^*/\partial d_1 < 0$, $\partial N_1^*/\partial d_2 > 0$, $\partial N_2^*/\partial d_1 > 0$, and $\partial N_2^*/\partial d_2 < 0$. Thus, points where $\partial N_j^*/\partial d_k > 0$ for all j, k can only arise if equations (C5) and (C6) are both positive. Note that $\bar{\Delta} > 0$ implies $b_{22}c_{22}/b_{21}c_{21} < b_{12}c_{12}/b_{11}c_{11}$, which implies $0 > \alpha_{12} - b_{22}c_{22}/b_{21}c_{21} > \alpha_{12} - b_{12}c_{12}/b_{11}c_{11}$. Hence, equations (C5) and (C6) cannot both be positive for the same value of α_{12} . The proof for the case where $\Delta < 0$ and $\bar{\Delta} < 0$ is similar. While stable coexistence does not occur when Δ and $\bar{\Delta}$ have opposite signs, a similar argument shows that the result holds for that case as well. \square

Appendix C.1 Effects of mortality perturbations on the equilibrium density of heterospecifics

The effects of small, controlled changes in the mortality rate of one species on the equilibrium density of the other species are determined by equations (C3) and (C4). For low levels of interspecific prey competition (α small), both equations are negative. As the level of interspecific prey competition increases, the derivatives increase. Equations (C3) and (C4) switch sign, respectively, at

$$\alpha_1 = q \frac{c_{11}b_{21}c_{21}k_2 + c_{12}b_{22}c_{22}k_1}{c_{12}b_{21}c_{21}k_1q^2 + c_{11}b_{22}c_{22}k_2} \quad (\text{C7})$$

$$\alpha_2 = q \frac{c_{21}b_{11}c_{11}k_2 + c_{22}b_{12}c_{12}k_1}{c_{21}b_{12}c_{12}k_2 + c_{22}b_{11}c_{11}k_1q^2}. \quad (\text{C8})$$

Consider the case where the conversion efficiencies are equal ($b_{ji} = 1$), interspecific prey competition is symmetric ($q = 1$), and intraspecific competition is equal ($k_1 = k_2$). In this case, the above values simplify to $\alpha_1 = \alpha_2 = (c_{12}c_{22} + c_{11}c_{21})/(c_{11}c_{22} + c_{12}c_{21})$. This was the value identified by Vandermeer (1980); below the value the indirect interaction between predators is competition and above the value the indirect interaction is mutualism. Under traditional resource partitioning, this value is always less than 1. Thus, for sufficiently high and symmetric interspecific prey competition, the indirect relationship will switch from competition to mutualism. Under defense-based partitioning, the value is always greater than one. Hence, under

defense-based partitioning, positive indirect interactions require some asymmetry in prey interspecific or intraspecific competition. Because contramensalism cannot arise if $q = 1$ and $k_1 = k_2$, these results suggest that contramensalism can arise when $b_{ji} = 1$ only if there is asymmetry in interspecific or intraspecific prey competition.

Allowing for unequal conversion efficiencies ($b_{ji} \neq 1$) alters the above results. When $b_{ji} \neq 1$, $q = 1$, and $k_1 = k_2$, the critical α values simplify to $\alpha_1 = (b_{12}c_{12}c_{22} + b_{11}c_{11}c_{21})/(b_{11}c_{11}c_{22} + b_{12}c_{12}c_{21})$ and $\alpha_2 = (c_{12}b_{22}c_{22} + c_{11}b_{21}c_{21})/(c_{11}b_{22}c_{22} + c_{12}b_{21}c_{21})$. Because the two critical values are not equal, contramensalism is possible when the conversion efficiencies are not equal, even when prey competition is symmetric. Note that $c_{j1} - c_{j2}$ and $b_{j1}c_{j1} - b_{j2}c_{j2}$ do not necessarily have the same sign. Indeed, different signs are expected when the predators only coexist with one prey in allopatry and have a sufficiently greater conversion efficiency for that prey. When $c_{j1} - c_{j2}$ and $b_{j1}c_{j1} - b_{j2}c_{j2}$ have the same sign, the critical values are less than 1 for traditional resource partitioning and greater than 1 for defense-based partitioning. This result is the same as in the $b_{ji} = 1$ case and implies that positive indirect interactions are not possible for defense-based partitioning. When $c_{j1} - c_{j2}$ and $b_{j1}c_{j1} - b_{j2}c_{j2}$ have opposite signs, predators have higher conversion efficiencies on the prey that they attack at a lower rate. In this case, it is possible that the critical values are greater than 1 for traditional resource partitioning and less than 1 for defense-based partitioning - this is the opposite of the previous result. In total, our results imply that when prey competition is symmetric ($q = 1$) and intraspecific competition is equal ($k_1 = k_2$), (i) positive indirect effects occur under defense-based partitioning only if predators have a much higher conversion efficiency on prey that they capture at a lower rate and (ii) contramensalism only occurs if the predators have unequal conversion efficiencies or if there is asymmetry in intra- or inter-specific prey competition.

In general, increasing the asymmetry in interspecific prey competition ($q \neq 1$) will cause the derivatives (C1) and (C2) to decrease. Thus, increased asymmetry promotes positive indirect interactions between the predators.

Appendix C.2 Effects of mortality perturbations controlled for self effects

Predator species one and two exhibit hydra effects when equations (C3) and (C4), respectively, are positive. When interspecific prey competition is sufficiently low (α small), equations (C3) and (C4) are both negative, implying neither species exhibits the hydra effect. As the level of interspecific competition increases, the derivatives increase and respectively change sign at:

$$\alpha_3 = q \frac{b_{21}c_{21}^2k_2 + b_{22}c_{22}^2k_1}{c_{21}c_{22}(b_{21}k_1q^2 + b_{22}k_2)} \quad (\text{C9})$$

$$\alpha_4 = q \frac{b_{11}c_{11}^2k_2 + b_{12}c_{12}^2k_1}{c_{11}c_{12}(b_{11}k_1q^2 + b_{12}k_2)} \quad (\text{C10})$$

Consider the case where the conversion efficiencies are equal ($b_{ji} = 1$), interspecific prey competition is symmetric ($q = 1$), and intraspecific competition is equal ($k_1 = k_2$). In this case the above critical values simplify to $(c_{11}^2 + c_{12}^2)/2c_{11}c_{12}$ and $(c_{21}^2 + c_{22}^2)/2c_{21}c_{22}$. Both of these values are always greater than 1. Thus, hydra effects cannot arise without some asymmetry in prey competition ($q \neq 1$ or $k_1 \neq k_2$) or different conversion efficiencies (b_{ji} different). If the conversion efficiencies are not equal (but $q = 1$ and $k_1 = k_2$), then the critical values are less than one when $c_{j1} - c_{j2}$ and $b_{j1}c_{j1} - b_{j2}c_{j2}$ have opposite signs. Thus, unequal conversion efficiencies do allow for hydra effects when prey competition is symmetric and equal, provided that the predators have higher conversion efficiencies for prey types for which they have lower attack rates. Greater asymmetry in interspecific prey competition ($q \neq 1$) increases the values of equations (C3) and (C4) regardless of the predator efficiencies or the level of intraspecific competition. Thus, greater asymmetry in interspecific prey competition promotes hydra effects. Also, hydra effects are more likely to occur if $b_{11} < b_{12}$ and/or $k_1 < k_2$ when $q \ll 1$ or if $b_{11} > b_{12}$ and/or $k_1 > k_2$ when $q \gg 1$ since those combinations of values maximize the denominators of the above critical values. In total, hydra effects are possible only when the predators have different conversion efficiencies or prey interspecific competition is sufficiently asymmetric.

If one predator is a specialist, meaning it only captures one of the prey, then the other predator cannot exhibit a hydra effect. For example, if predator N_1 cannot capture one of the two prey species ($c_{11} = 0$ or $c_{12} = 0$), then predator N_2 cannot exhibit a hydra effect. Similarly, if predator N_2 cannot capture one of the two prey species ($c_{21} = 0$ or $c_{22} = 0$), then predator N_1 cannot exhibit a hydra effect ($\alpha_3 > 1$). We note that if the predator can capture both prey, but only utilizes one, e.g., $c_{11} > 0$ and $b_{11} = 0$, then the other predator can exhibit hydra effects.

As noted in the main text, correcting for hydra effects can change the inferred indirect interaction between predators. Taking the appropriate ratios of equations (C1) through (C4) yields

$$\frac{dN_1^*}{dN_2^*} = \left(\frac{\partial N_1^*}{\partial d_2} \right) / \left(\frac{\partial N_2^*}{\partial d_2} \right) = \frac{-k_1 c_{22} (b_{12} c_{12} - b_{11} c_{11} \alpha q) - k_2 c_{21} (b_{11} c_{11} - b_{12} c_{12} \alpha / q)}{k_2 c_{11} (b_{11} c_{11} - b_{12} c_{12} \alpha / q) + k_1 c_{12} (b_{12} c_{12} - b_{11} c_{11} \alpha q)} \quad (\text{C11})$$

$$\frac{dN_2^*}{dN_1^*} = \left(\frac{\partial N_2^*}{\partial d_1} \right) / \left(\frac{\partial N_1^*}{\partial d_1} \right) = \frac{-k_1 c_{12} (b_{22} c_{22} - b_{21} c_{21} \alpha q) - k_2 c_{11} (b_{21} c_{21} - b_{22} c_{22} \alpha / q)}{k_2 c_{21} (b_{21} c_{21} - b_{22} c_{22} \alpha / q) + k_1 c_{22} (b_{22} c_{22} - b_{21} c_{21} \alpha q)} \quad (\text{C12})$$

Note that setting the conversion rates equal yields equations (6) and (7) of the main text. Also note that the inferred interactions for each region of parameter space in Table 1 of the main text are the same for the $b_{ji} = 1$ and $b_{ji} \neq 1$ cases. The derivatives

(C11) and (C12) switch signs, respectively, at the critical values

$$\alpha_5 = \frac{c_{21}b_{11}c_{11}k_2 + c_{22}b_{12}c_{12}k_1}{c_{22}b_{11}c_{11}k_1q + c_{21}b_{12}c_{12}k_2/q} \quad (\text{C13})$$

$$\alpha_6 = \frac{c_{11}b_{21}c_{21}k_2 + c_{12}b_{22}c_{22}k_1}{c_{12}b_{21}c_{21}k_1q + c_{11}b_{22}c_{22}k_2/q}, \quad (\text{C14})$$

respectively.

As noted in the main text, if the conversion efficiencies are equal ($b_{ji} = 1$), interspecific prey competition is symmetric ($q = 1$), and intraspecific competition is equal ($k_1 = k_2$), then the derivatives (C11) and (C12) switch signs at the same value: $\alpha = (c_{12}c_{22} + c_{11}c_{21})/(c_{11}c_{22} + c_{12}c_{21})$. Note that under defense-based resource partitioning, the critical value of α is always greater than 1. Due to the similarity of the terms in the numerators and denominators of equations (C11) and (C12), both derivatives tend to be negative when interspecific prey competition is high ($\alpha \approx 1$) and highly asymmetric ($q \ll 1$ or $q \gg 1$), regardless of the level of intraspecific competition or the conversion efficiencies. The same holds for very low levels of interspecific prey competition ($\alpha \approx 0$). Thus, positive indirect effects between predators are promoted at intermediate levels of asymmetry in interspecific prey competition.

Asymmetry in intraspecific prey competition ($k_1 \neq k_2$) can also influence the sign of the interaction, though to a lesser extent than asymmetry in interspecific prey competition. To see this, consider the case where interspecific competition is symmetric and complete ($q = 1$ and $\alpha = 1$). In this case the derivatives simplify to

$$\frac{dN_1}{dN_2} = \frac{c_{22}k_1 - c_{21}k_2}{c_{11}k_2 - c_{12}k_1}, \quad \frac{dN_2}{dN_1} = \frac{c_{12}k_1 - c_{11}k_2}{c_{21}k_2 - c_{22}k_1}. \quad (\text{C15})$$

Note that in this special case the derivatives are inverses, implying they have the same sign. Mutually positive indirect effects occur when either $c_{11}/c_{12} < k_1/k_2 < c_{21}/c_{22}$ or $c_{11}/c_{12} > k_1/k_2 > c_{21}/c_{22}$. Mutually negative indirect effects occur when one of the inequalities in either expression is reversed. The inequalities specify that the ratio of the strength of prey one's intraspecific competition to that of prey two (k_1/k_2) lies between the ratios of the each predator's capture rates. Note that only the second expression can be satisfied under traditional resource partitioning and that only the first expression can be satisfied under defense-based partitioning. While the range of k_1/k_2 values yielding mutually positive indirect effects is narrow when the two predators have similar ratios of capture rates, the range of predator parameters allowing coexistence is also narrow under those circumstances. When predators differ sufficiently in their capture rates to allow coexistence over a wide range of their demographic parameters (e.g., b_{ji}, d_{ji}), there is also a wide range of k_1/k_2 values that allow mutually positive indirect interactions.

Appendix C.3 Relation to Chesson and Kuang (2008) approach

The indirect interactions inferred using methods 1 and 2 (which represent changes in equilibrium density) are very closely related to the competition coefficients (which represent effects on per capita growth rates) derived using the methods developed in MacArthur (1970) and Chesson and Kuang (2008). Here we show that connection.

The approach developed in MacArthur (1970) and Chesson and Kuang (2008) assumes that the dynamics of the prey (R_1, R_2) are much faster than the dynamics of the predators (N_1, N_2). In this fast-slow limit, the prey dynamics tend to equilibrium very quickly and respond nearly instantaneously to changes in the predator densities. Mathematically, the dynamics of the fast-slow system are determined by setting the right hand sides of the dR_1/dt and dR_2/dt equations of model (1) equal to zero, solving for R_1 and R_2 , and substituting the values of R_1 and R_2 into the dN_1/dt and dN_2/dt equations of model (1). This results in a two-species Lotka-Volterra model,

$$\frac{dN_1}{dt} = N_1(\beta_1 + \sigma_{11}N_1 + \sigma_{12}N_2) \quad (\text{C16})$$

$$\frac{dN_2}{dt} = N_2(\beta_2 + \sigma_{21}N_1 + \sigma_{22}N_2). \quad (\text{C17})$$

The intraspecific and interspecific predator competition coefficients in model (C16) are related to the derivatives (C1) through (C4) of model (1) in the following way

$$\begin{aligned} \sigma_{11} &= \frac{\partial N_2^*}{\partial d_2} \frac{\Delta \bar{\Delta}}{k_1 k_2 (1 - \alpha^2)} \\ \sigma_{12} &= \frac{\partial N_1^*}{\partial d_2} \frac{-\Delta \bar{\Delta}}{k_1 k_2 (1 - \alpha^2)} \\ \sigma_{21} &= \frac{\partial N_2^*}{\partial d_1} \frac{-\Delta \bar{\Delta}}{k_1 k_2 (1 - \alpha^2)} \\ \sigma_{22} &= \frac{\partial N_1^*}{\partial d_1} \frac{\Delta \bar{\Delta}}{k_1 k_2 (1 - \alpha^2)}. \end{aligned} \quad (\text{C18})$$

The β_i are given by

$$\begin{aligned} \beta_1 &= \frac{b_{11}c_{11}(k_2r_1 - k_1r_2\alpha/q) + b_{12}c_{12}(k_1r_2 - k_2r_2\alpha/q)}{k_1k_2(1 - \alpha^2)} - d_1 \\ \beta_2 &= \frac{b_{21}c_{21}(k_2r_1 - k_1r_2\alpha/q) + b_{22}c_{22}(k_1r_2 - k_2r_2\alpha/q)}{k_1k_2(1 - \alpha^2)} - d_2. \end{aligned} \quad (\text{C19})$$

The relations between the interspecific competition coefficients in model (C16) and the derivatives (C1) and (C2) of model (1) imply that the indirect effects measured using method 1 are proportional to the direct effects predators have on each other's per

capita growth rate in model (C16). The ratios σ_{12}/σ_{11} and σ_{21}/σ_{22} are the traditional relative interaction coefficients for the Lotka-Volterra model (C16). These ratios are identical to the indirect effects measured using method 2.

In total, the derivatives (C1) through (C4) of model (1) that define the indirect effects measured using methods 1 and 2 can be interpreted as interspecific and intraspecific competition coefficients of a two-species Lotka-Volterra model where the predators have direct effects on each other. We note though that while this approach can be helpful in interpreting the signs and magnitudes of the derivatives, the fast prey dynamics assumption may not be appropriate in many cases, particularly those where the four-species model (1) exhibits cyclic dynamics.

Appendix C.4 Non-selective mortality perturbations

We are interested in the effects of small, controlled increases in indiscriminate mortality on the total equilibrium density of the top trophic level, $N_{tot} = N_1^* + N_2^*$. For each species, we can write $d_j = d + \delta_j$ where d is the mortality rate due to indiscriminate mortality in the system and δ_j is the mortality rate due to species specific factors. The response of the total equilibrium density of the trophic level to changes in the indiscriminate mortality rate is given by

$$\begin{aligned} \frac{\partial N_{tot}}{\partial d} &= \frac{\partial N_2^*}{\partial d_1} + \frac{\partial N_1^*}{\partial d_2} + \frac{\partial N_1^*}{\partial d_1} + \frac{\partial N_2^*}{\partial d_2} \\ &= \frac{1}{\Delta\Delta} [k_1(c_{12} - c_{22})(b_{11}c_{11} - b_{21}c_{21})\alpha q + k_2(c_{11} - c_{21})(b_{12}c_{12} - b_{22}c_{22})\alpha/q] \\ &\quad + \frac{1}{\Delta\Delta} [-k_2(c_{11} - c_{21})(b_{11}c_{11} - b_{21}c_{21}) - k_1(c_{12} - c_{22})(b_{12}c_{12} - b_{22}c_{22})] \quad (C20) \end{aligned}$$

which is the sum of equations (C1) through (C4). When equation (C20) is positive, the total predator equilibrium density increases as indiscriminate mortality increases, i.e., there is a trophic-level hydra effect.

In general, a trophic-level hydra effect does not imply hydra effects in each species individually. Conversely, when both predators exhibit hydra effects due to species-specific mortality, their summed equilibrium densities need not increase with greater indiscriminate mortality. A particular numerical example illustrating the above is the parameter set $\{r_1 = r_2 = k_1 = k_2 = 1, c_{11} = 0.5, c_{12} = 1.5, c_{21} = 1.5, c_{22} = 2, d_1 = 0.25, d_2 = 0.5, q = 5\}$. Because cycles occur for $\alpha > 0.408$, we focus on average predator densities. For $\alpha < 0.48077$, increased indiscriminate mortality causes the total predator equilibrium density to decrease. For $\alpha > 0.48077$, the total predator equilibrium density increases. For $\alpha > 0.246305$, predator one increases with indiscriminate mortality whereas for $\alpha < 0.16556$ predator two increases. The trophic-level hydra effect occurs for large α because the increase in predator one is greater than the decrease in predator two. For predator-specific mortality perturbations, predator one increases with its own mortality rate for $\alpha > 0.40064$ and predator two increases with its own mortality rate for $\alpha > 0.64103$.

Trophic-level hydra effects can occur under traditional or defense-based partitioning. When a trophic-level hydra effect occurs under defense-based partitioning, then it is possible for both or only one predator species to increase in abundance. In the latter case, the equilibrium density of one species increases and the equilibrium density of the other decreases, but the total number of predators increases. In contrast, when a trophic-level hydra effect occurs in a system with traditional resource partitioning, it is always that case that the equilibrium densities of the two predators change in opposite directions. For example, consider the parameter values: $r_1 = k_1 = 1.9$, $r_2 = k_2 = 5.5$, $c_{11} = 4.8$, $c_{12} = 4.1$, $c_{21} = 6.6$, $c_{22} = 7.5$, $d_1 = 3.6$, $d_2 = 6.4$, $\alpha_{12} = 0.68$, $\alpha_{21} = 0.96$. In this case with traditional resource partitioning, a trophic-level hydra effect occurs and the equilibrium density of predator 1 increases whereas the equilibrium density of predator 2 decreases. Stated mathematically, our general result is that with traditional resource partitioning it is not possible for $\frac{\partial N_1^*}{\partial d_1} + \frac{\partial N_1^*}{\partial d_2}$ and $\frac{\partial N_2^*}{\partial d_1} + \frac{\partial N_2^*}{\partial d_2}$ to both be positive; see the proof below.

Theorem 2. *Assume $c_{22} - c_{21} > 0$, $c_{11} - c_{12} > 0$, $b_{22}c_{22} - b_{12}c_{12} > 0$, $b_{11}c_{11} - b_{21}c_{21} > 0$, and $\Delta, \bar{\Delta} < 0$. Then $\frac{\partial N_1^*}{\partial d_1} + \frac{\partial N_1^*}{\partial d_2}$ and $\frac{\partial N_2^*}{\partial d_1} + \frac{\partial N_2^*}{\partial d_2}$ cannot both be positive.*

Proof. For presentational purposes, in this proof we will use the notation α_{ij} to denote the interspecific prey competition coefficients. Recall that $\alpha_{12} = \alpha q$ and $\alpha_{21} = \alpha/q$.

Solving the inequalities $\partial N_1^*/\partial d_1 + \partial N_1^*/\partial d_2 > 0$ and $\partial N_2^*/\partial d_1 + \partial N_2^*/\partial d_2 > 0$ for α_{21} yields

$$\begin{aligned} \alpha_{21} &< \frac{k_1 c_{22}(b_{22}c_{22} - b_{12}c_{12}) + (b_{21}c_{21} - b_{11}c_{11})(k_2 c_{21} - k_1 c_{22} \alpha_{12})}{k_2 c_{21}(b_{22}c_{22} - b_{12}c_{12})} && \text{if } \frac{k_2 c_{21}(b_{22}c_{22} - b_{12}c_{12})}{\Delta \bar{\Delta}} < 0 \\ \alpha_{21} &> \frac{k_1 c_{22}(b_{22}c_{22} - b_{12}c_{12}) + (b_{21}c_{21} - b_{11}c_{11})(k_2 c_{21} - k_1 c_{22} \alpha_{12})}{k_2 c_{21}(b_{22}c_{22} - b_{12}c_{12})} && \text{if } \frac{k_2 c_{21}(b_{22}c_{22} - b_{12}c_{12})}{\Delta \bar{\Delta}} > 0 \\ \alpha_{21} &> \frac{(b_{11}c_{11} - b_{21}c_{21})(\alpha_{12}c_{12}k_1 - k_2 c_{11}) + c_{12}k_1(b_{22}c_{22} - b_{12}c_{12})}{c_{11}k_2(b_{22}c_{22} - b_{12}c_{12})} && \text{if } \frac{k_2 c_{11}(b_{22}c_{22} - b_{12}c_{12})}{\Delta \bar{\Delta}} < 0 \\ \alpha_{21} &< \frac{(b_{11}c_{11} - b_{21}c_{21})(\alpha_{12}c_{12}k_1 - k_2 c_{11}) + c_{12}k_1(b_{22}c_{22} - b_{12}c_{12})}{c_{11}k_2(b_{22}c_{22} - b_{12}c_{12})} && \text{if } \frac{k_2 c_{11}(b_{22}c_{22} - b_{12}c_{12})}{\Delta \bar{\Delta}} > 0. \end{aligned} \tag{C21}$$

Combining the first lines of equations (C21) and (C22) and combining the second lines of those equations yields, respectively,

$$\begin{aligned} \alpha_{12} &< \frac{b_{22}c_{22} - b_{12}c_{12}}{b_{21}c_{21} - b_{11}c_{11}} && \text{if } 0 < \frac{k_1 \Delta (b_{11}c_{11} - b_{21}c_{21})}{c_{11}k_2 c_{21}(b_{12}c_{12} - b_{22}c_{22})} \\ \alpha_{12} &> \frac{b_{22}c_{22} - b_{12}c_{12}}{b_{21}c_{21} - b_{11}c_{11}} && \text{if } 0 > \frac{k_1 \Delta (b_{11}c_{11} - b_{21}c_{21})}{c_{11}k_2 c_{21}(b_{12}c_{12} - b_{22}c_{22})}. \end{aligned} \tag{C23}$$

In the following we set $\alpha_{12} = (b_{22}c_{22} - b_{12}c_{12})/(b_{21}c_{21} - b_{11}c_{11}) + \epsilon$.

We assume $\Delta, \bar{\Delta} < 0$ and $(b_{22}c_{22} - b_{12}c_{12}) > 0$. Substitution into the appropriate conditions from equations (C21) and (C22) yields

$$\frac{c_{22}k_1(b_{11}c_{11} - b_{21}c_{21})}{c_{21}k_2(b_{22}c_{22} - b_{12}c_{12})}\epsilon + \frac{b_{21}c_{21} - b_{11}c_{11}}{b_{22}c_{22} - b_{12}c_{12}} < \alpha_{21} < \frac{c_{12}k_1(b_{11}c_{11} - b_{21}c_{21})}{c_{11}k_2(b_{22}c_{22} - b_{12}c_{12})}\epsilon + \frac{(b_{11}c_{11} - b_{21}c_{21})}{(b_{12}c_{12} - b_{22}c_{22})}. \quad (\text{C24})$$

In the traditional resource partitioning case we have that $b_{22}c_{22} - b_{12}c_{12} > 0$, $b_{11}c_{11} - b_{21}c_{21} > 0$, $\bar{\Delta} < 0$, and $\Delta < 0$. Via the first line of equation (C23), $\epsilon < 0$, which implies that the right hand side of equation (C24) is always negative. Hence inequalities (C21) and (C22) cannot both be satisfied. \square

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