

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 E Comparisons of allopatric and sympatric densities and extinction sequences induced via increased mortality

Appendix E.1 Summary of approach and results

The sympatric density for each predator is determined by its equilibrium density at P_4 . The allopatric density for N_j is determined by the equilibrium density at either $P_{R_1N_j}$, $P_{R_2N_j}$, or P_{3,N_j} . The equilibrium to be used is determined by the unique globally stable attractor in the three-species subsystem with N_j , R_1 , and R_2 . (Recall from appendix B that bistability in the three-species subsystem prevents coexistence of all four species.) If all three species coexist, then the allopatric density is determined by P_{3,N_j} . If stable coexistence of all three species is not possible, then the allopatric density is determined by (i) $P_{R_iN_j}$ where $i \neq j$ when $\Delta, \bar{\Delta} < 0$ or (ii) $P_{R_iN_j}$ where $i = j$ when $\Delta, \bar{\Delta} > 0$. Recall that we assume Δ and $\bar{\Delta}$ have the same sign. For the remainder of this section, unless otherwise stated, we use allopatric density to refer to the density at the equilibrium that is globally stable in the three-species subsystem.

To make analytical predictions about the relations between the allopatric and sympatric densities, we use the derivatives $\partial N_j^* / \partial d_k$. To do this we start with parameter set p^* where the coexistence equilibrium P_4 exists and then determine how the densities at P_4 and the densities at the boundary equilibria change as one of the mortality rates is increased or decreased. If the densities at P_4 and the boundary equilibria change in opposite directions, we can determine the relations between the sympatric and allopatric densities for the parameter set p^* . For example, assume that as d_2 is increased, the density of N_2 at P_4 increases, the density of N_2 at P_{3,N_2} decreases, and N_1 goes extinct before any prey species go extinct. Then we know that the density of N_2 at P_4 is less than the density of N_2 at P_{3,N_2} for the parameter

set p^* . If the densities at the equilibria change in the same way, then we cannot determine the relations between the allopatric and sympatric densities. For instance, if instead the densities of N_2 at P_4 and P_{3,N_2} increase as d_2 is increased, then we cannot determine which density is larger using this method.

All of our analytical results are presented at the end of this subsection in theorems 1 and 2. Those results are summarized in Tables E1 and E2, respectively, where parameter space is partitioned based on the signs of equations (C1) through (C4). Note that many of the conditions in Tables E1 and E2 involving the two-species equilibria $P_{R_i N_j}$ hold only if P_{3,N_j} has negative entries. When P_{3,N_j} is a saddle point with positive entries, one of the two-species equilibria $P_{R_i N_j}$ will be globally attracting. In these cases, the allopatric density at that globally attracting equilibrium can be greater than or less than the sympatric density at P_4 . Exceptions, where the relations between the densities at $P_{R_i N_j}$ and P_4 are independent of the positivity of P_{3,N_j} , are denoted by daggers (\dagger) in Tables E1 and E2.

Also note that while the proofs of our results depend on the signs of Δ and $\bar{\Delta}$, the interpretation of the results is the same for both cases. Our general results are summarized in Table E3 where we list all possible relations between the allopatric and sympatric densities for each region of parameter space defined by the signs of equations (C1) through (C4). In some regions of parameter space the relations between the allopatric and sympatric densities can always be determined for one or both predators. The allopatric densities are always higher than the sympatric densities for both predators in the regions defined by the sign structures $\{++--\}$, $\{+++-\}$, and $\{++-+\}$. For all of the rows in Table E3 where mutualism is not listed as a possible interaction (e.g., the third row denoted by $\{-++-\}$), the allopatric density is always higher than the sympatric density for at least one predator. Note that for the regions where mutualism is a possibility, the relations between the allopatric and sympatric densities are not constant throughout the region of parameter space and it is possible to infer any of the indirect interactions in those regions.

Table E1: Relations between the allopatric and sympatric equilibrium densities when $\Delta, \bar{\Delta} > 0$

Region*	$P_{R_1 N_1}$ Density**	$P_{R_2 N_1}$ Density**	P_{3, N_1} Density	$P_{R_1 N_2}$ Density**	$P_{R_2 N_2}$ Density**	P_{3, N_2} Density
{+ + --}	$\bar{N}_1(P_{R_1 N_1}) > N_1$		$\hat{N}_1(P_{3, N_1}) > N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2$
{+ + +-}	$\bar{N}_1(P_{R_1 N_1}) > N_1$	$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2$
{- + +-}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2$
{- - +-}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2$		$\hat{N}_2(P_{3, N_2}) > N_2$
{- + ++}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2$	$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- - ++}		$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2$		$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- + --}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2$
{- + -+}		$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2$	$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- - -+}		$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2^\dagger$
{- + -+}	$\bar{N}_1(P_{R_1 N_1}) > N_1$	$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2$		$\hat{N}_2(P_{3, N_2}) > N_2$
{+ - ++}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$	$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{+ + -+}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$	$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{+ - --}	$\bar{N}_1(P_{R_1 N_1}) > N_1$		$\hat{N}_1(P_{3, N_1}) > N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2$
{- - --}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2$
{+ - -+}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2^\dagger$

N_1 and N_2 denote the sympatric equilibrium densities at P_4 . $\bar{N}_1(\cdot)$ and $\bar{N}_2(\cdot)$ denote the allopatric equilibrium densities at the two-species equilibria. $\hat{N}_1(\cdot)$ and $\hat{N}_2(\cdot)$ denote the allopatric equilibrium densities at the three-species equilibria.

*Regions of parameter space are defined by the signs of the derivatives in equations (C1) through (C4), respectively.

** Comparisons involving the two species equilibria (i.e., $N_j(P_{R_i N_j}) > N_j$) are guaranteed to hold only if the equilibrium $N_j(P_{3, N_j})$ does not exist. Exceptions are denoted by \dagger , i.e., \dagger denote relations between $N_j(P_{R_i N_j})$ and N_j that always hold.

\ddagger The determinant of the Jacobian evaluated at P_{3, N_j} is positive, implying that generic solutions will tend to one of the two species equilibria. Because of this, the relation between the three-species allopatric density and sympatric density is not biologically meaningful.

Table E2: Relations between the allopatric and sympatric equilibrium densities when $\Delta, \bar{\Delta} < 0$

Region*	$P_{R_1 N_1}$ Density**	$P_{R_2 N_1}$ Density**	P_{3, N_1} Density	$P_{R_1 N_2}$ Density*	$P_{R_2 N_2}$ Density**	P_{3, N_2} Density
{+ + --}		$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2$		$\hat{N}_2(P_{3, N_2}) > N_2$
{+ + +-}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$	$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2$
{- + +-}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$		$\hat{N}_2(P_{3, N_2}) < N_2$
{- - +-}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2$
{- + ++}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$	$\bar{N}_2(P_{R_1 N_2}) > N_2^\dagger$	$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- - ++}	$\bar{N}_1(P_{R_1 N_1}) > N_1$		$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- + --}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2$		$\hat{N}_2(P_{3, N_2}) > N_2$
{- + -+}	$\bar{N}_1(P_{R_1 N_1}) > N_1$		$\hat{N}_1(P_{3, N_1}) > N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2$	$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{- - -+}	$\bar{N}_1(P_{R_1 N_1}) > N_1$		$\hat{N}_1(P_{3, N_1}) > N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2^\dagger$
{+ - +-}	$\bar{N}_1(P_{R_1 N_1}) > N_1$	$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2$	$\hat{N}_2(P_{3, N_2}) > N_2$
{+ - ++}	$\bar{N}_1(P_{R_1 N_1}) > N_1$	$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1^\dagger$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{+ + -+}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1$	$\bar{N}_2(P_{R_1 N_2}) > N_2$	$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) > N_2^\dagger$
{+ - --}		$\bar{N}_1(P_{R_2 N_1}) > N_1$	$\hat{N}_1(P_{3, N_1}) > N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2$
{- - --}	$\bar{N}_1(P_{R_1 N_1}) > N_1^\dagger$		$\hat{N}_1(P_{3, N_1}) < N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2$
{+ - -+}		$\bar{N}_1(P_{R_2 N_1}) > N_1^\dagger$	$\hat{N}_1(P_{3, N_1}) < N_1$		$\bar{N}_2(P_{R_2 N_2}) > N_2^\dagger$	$\hat{N}_2(P_{3, N_2}) < N_2^\dagger$

N_1 and N_2 denote the sympatric equilibrium densities at P_4 . $\bar{N}_1(\cdot)$ and $\bar{N}_2(\cdot)$ denote the allopatric equilibrium densities at the two-species equilibria. $\hat{N}_1(\cdot)$ and $\hat{N}_2(\cdot)$ denote the allopatric equilibrium densities at the three-species equilibria.

*Regions of parameter space are defined by the signs of the derivatives in equations (C1) through (C4), respectively.

** Comparisons involving the two species equilibria (i.e., $N_j(P_{R_i N_j}) > N_j$) are guaranteed to hold only if the equilibrium $N_j(P_{3, N_j})$ does not exist. Exceptions are denoted by \dagger , i.e., \dagger denote relations between $N_j(P_{R_i N_j})$ and N_j that always hold.

‡ The determinant of the Jacobian evaluated at P_{3, N_j} is positive, implying that generic solutions will tend to one of the two species equilibria. Because of this, the relation between the three-species allopatric density and sympatric density is not biologically meaningful.

Table E3: Possible relations between allopatric and sympatric densities and the resulting inferred indirect interaction

Region*	Possible N_1 Relations	Possible N_2 Relations	Classifications [†]
{+ + --}	Allop. > Symp.	Allop. > Symp.	Comp.
{+ + +-}	Allop. > Symp.	Allop. > Symp.	Comp.
{- + +-}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.	Comp., Contra.
{- - +-}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra., Mut.
{- + ++}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.	Comp., Contra.
{- - ++}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra., Mut.
{- + --}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.	Comp., Contra.
{- + -+}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.	Comp., Contra.
{- - -+}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra., Mut.
{+ - +-}	Allop. > Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra.
{+ - ++}	Allop. > Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra.
{+ + -+}	Allop. > Symp.	Allop. > Symp.	Comp.
{+ - --}	Allop. > Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra.
{- - --}	Allop. > Symp.; Allop. < Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra., Mut.
{+ - -+}	Allop. > Symp.	Allop. > Symp.; Allop. < Symp.	Comp., Contra.

Entries in columns 2 and 3 that have multiple relations imply that the allopatric density can be higher or lower than the sympatric density in that region.

*Regions of parameter space are defined by the signs of the derivatives in equations (C1) through (C4), respectively.

[†] Classifications are indirect competition (Comp.), indirect mutualism (Mut.), and indirect contramensalism (Contra.).

Appendix E.2 Statement and proof of results

Here we present our analytical results about the relations between the allopatric and sympatric densities of the predators. Each theorem presents the relations between the allopatric and sympatric based on the signs of the derivatives (C1) through (C4). Theorem 1 addresses the case where $\bar{\Delta} > 0$. Theorem 2 addresses the case where $\bar{\Delta} < 0$. Due to the similarity of the proofs, only the proof for statement (a) of theorem 1 is presented at the end of this subsection.

Theorem 1. *Assume $\bar{\Delta} > 0$. Let p^* denote a parameter set such that P_4 has positive entries and let d_1^* and d_2^* denote the predator mortality rates. Denote the entries of P_4 by $[R_1^*(P_4), R_2^*(P_4), N_1^*(P_4), N_2^*(P_4)]$. Let $d_{1,l} \leq d_1^* \leq d_{1,h}$ denote the range of d_1 values such that $N_1^*(P_4)$ and $N_2^*(P_4)$ are nonnegative for all other parameters fixed at p^* . Let $d_{2,l} \leq d_2^* \leq d_{2,h}$ denote the range of d_2 values such that $N_1^*(P_4)$ and $N_2^*(P_4)$ are nonnegative for all other parameters fixed at p^* . Let $P_{3,N_j}(d_j) = [\hat{R}_1(P_{3,N_j}, d_j), \hat{R}_2(P_{3,N_j}, d_j), \hat{N}_j(P_{3,N_j}, d_j)]$ denote the solution to $\{\frac{1}{R_1} \frac{dR_1}{dt} = 0, \frac{1}{R_2} \frac{dR_2}{dt} = 0, \frac{1}{N_j} \frac{dN_j}{dt} = 0\}$ where the mortality rate of N_j is d_j and all other parameters are fixed at p^* . Note that $P_{3,N_j}(d_j)$ may have non-positive entries. Denote the entries of the boundary equilibria $P_{R_i N_j}$ for p^* by $[\bar{R}_i(P_{R_i N_j}), \bar{N}_j(P_{R_i N_j})]$. Let $\delta = -\partial N_2^*/\partial d_2(P_4)$ and $\bar{\delta} = -\partial N_1^*/\partial d_1(P_4)$.*

- (a) *Assume $\partial N_1^*/\partial d_1 < 0$ and $\partial N_2^*/\partial d_1 > 0$ at P_4 . (i) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. Otherwise, $\bar{N}_2(P_{R_2 N_2}) > N_2^*(P_4)$. (ii) If $\Delta \bar{\Delta}(1 - \alpha^2)/\delta < 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$.*
- (b) *Assume $\partial N_1^*/\partial d_1 > 0$ and $\partial N_2^*/\partial d_1 > 0$ at P_4 . (i) Then $\bar{N}_1(P_{R_2 N_1}) > N_1^*(P_4)$ and $\bar{N}_2(P_{R_2 N_2}) > N_2^*(P_4)$. (ii) If $\Delta \bar{\Delta}(1 - \alpha^2)/\delta > 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$. (iii) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$.*
- (c) *Assume $\partial N_1^*/\partial d_1 > 0$ and $\partial N_2^*/\partial d_1 < 0$ at P_4 . (i) If $\Delta \bar{\Delta}(1 - \alpha^2)/\delta > 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_1^*, d_{1,h}]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$. If $P_{3,N_1}(d_1)$ has non-positive entries for some $d_1 \in [d_1^*, d_{1,h}]$, then $\bar{N}_1(P_{R_2 N_1}) > N_1^*(P_4)$. (ii) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. Otherwise, $\bar{N}_2(P_{R_1 N_2}) > N_2^*(P_4)$.*
- (d) *Assume $\partial N_1^*/\partial d_1 < 0$ and $\partial N_2^*/\partial d_1 < 0$ at P_4 . (i) $\bar{N}_2(P_{R_1 N_2}) > N_2^*(P_4)$. (ii) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$. (iii) If $\Delta \bar{\Delta}(1 - \alpha^2)/\delta < 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_1^*, d_{1,h}]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$.*
- (e) *Assume $\partial N_1^*/\partial d_2 > 0$ and $\partial N_2^*/\partial d_2 < 0$ at P_4 . If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$. Otherwise, $\bar{N}_1(P_{R_1 N_1}) > N_1^*(P_4)$. (ii) If $\Delta \bar{\Delta}(1 -$*

$\alpha^2)/\bar{\delta} < 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_{2,l}, d_2^*]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$.

- (f) Assume $\partial N_1^*/\partial d_2 > 0$ and $\partial N_2^*/\partial d_2 > 0$ at P_4 . (i) Then $\bar{N}_1(P_{R_1N_1}) > N_1^*(P_4)$ and $\bar{N}_2(P_{R_1N_2}) > N_2^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} > 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_{2,l}, d_2^*]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$. (iii) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$.
- (g) Assume $\partial N_1^*/\partial d_2 < 0$ and $\partial N_2^*/\partial d_2 > 0$ at P_4 . (i) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} > 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_2^*, d_{2,h}]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. If $P_{3,N_2}(d_2)$ has non-positive entries for some $d_2 \in [d_2^*, d_{2,h}]$, then $\bar{N}_2(P_{R_1N_2}) > N_2^*(P_4)$. (ii) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$. Otherwise, $\bar{N}_1(P_{R_2N_1}) > N_1^*(P_4)$.
- (h) Assume $\partial N_1^*/\partial d_2 < 0$ and $\partial N_2^*/\partial d_2 < 0$ at P_4 . (i) $\bar{N}_1(P_{R_2N_1}) > N_1^*(P_4)$. (ii) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$. (iii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} < 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_2^*, d_{2,h}]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$.

Theorem 2. Assume $\bar{\Delta} < 0$. Let p^* denote a parameter set such that P_4 has positive entries and let d_1^* and d_2^* denote the predator mortality rates. Denote the entries of P_4 by $[R_1^*(P_4), R_2^*(P_4), N_1^*(P_4), N_2^*(P_4)]$. Let $d_{1,l} < d_1^* < d_{1,h}$ denote the range of d_1 values such that $N_1^*(P_4)$ and $N_2^*(P_4)$ are nonnegative for all other parameters fixed at p^* . Let $d_{2,l} < d_2^* < d_{2,h}$ denote the range of d_2 values such that $N_1^*(P_4)$ and $N_2^*(P_4)$ are nonnegative for all other parameters fixed at p^* . Let $P_{3,N_j}(d_j) = [R_1^*(P_{3,N_j}, d_j), R_2^*(P_{3,N_j}, d_j), N_j^*(P_{3,N_j}, d_j)]$ denote the solution to $\{\frac{1}{R_1} \frac{dR_1}{dt} = 0, \frac{1}{R_2} \frac{dR_2}{dt} = 0, \frac{1}{N_j} \frac{dN_j}{dt} = 0\}$ where the mortality rate of N_j is d_j and all other parameters are fixed at p^* . Note that $P_{3,N_j}(d_j)$ may have non-positive entries. Denote the entries of the boundary equilibria $P_{R_iN_j}$ for p^* by $[\bar{R}_i(P_{R_iN_j}), \bar{N}_j(P_{R_iN_j})]$. Let $\delta = -\partial N_2^*/\partial d_2(P_4)$ and $\bar{\delta} = -\partial N_1^*/\partial d_1(P_4)$.

- (a) Assume $\partial N_1^*/\partial d_1 < 0$ and $\partial N_2^*/\partial d_1 > 0$ at P_4 . (i) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. Otherwise, $\bar{N}_2(P_{R_1N_2}) > N_2^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} < 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$.
- (b) Assume $\partial N_1^*/\partial d_1 > 0$ and $\partial N_2^*/\partial d_1 > 0$ at P_4 . (i) Then $\bar{N}_1(P_{R_1N_1}) > N_1^*(P_4)$ and $\bar{N}_2(P_{R_1N_2}) > N_2^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} > 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$. (iii) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$.
- (c) Assume $\partial N_1^*/\partial d_1 > 0$ and $\partial N_2^*/\partial d_1 < 0$ at P_4 . (i) If $P_{3,N_2}(d_2)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. Otherwise, $\bar{N}_2(P_{R_2N_2}) > N_2^*(P_4)$. (ii) If

$\Delta\bar{\Delta}(1 - \alpha^2)/\delta > 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_1^*, d_{1,h}]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$. If $P_{3,N_1}(d_1)$ has non-positive entries for some $d_1 \in [d_1^*, d_{1,h}]$, then $\bar{N}_1(P_{R_1N_1}) > N_1^*(P_4)$.

- (d) Assume $\partial N_1^*/\partial d_1 < 0$ and $\partial N_2^*/\partial d_1 < 0$ at P_4 . (i) $\bar{N}_2(P_{R_2N_2}) > N_2^*(P_4)$. (ii) If $P_{3,N_2}(d_2^*)$ has positive entries, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$. (iii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\delta < 0$ and $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_1^*, d_{1,h}]$, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$.
- (e) Assume $\partial N_1^*/\partial d_2 > 0$ and $\partial N_2^*/\partial d_2 < 0$ at P_4 . (i) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) > N_1^*(P_4)$. Otherwise, $\bar{N}_1(P_{R_1N_1}) > N_2^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} < 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_{2,l}, d_2^*]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$.
- (f) Assume $\partial N_1^*/\partial d_2 > 0$ and $\partial N_2^*/\partial d_2 > 0$ at P_4 . (i) Then $\bar{N}_1(P_{R_2N_1}) > N_1^*(P_4)$ and $\bar{N}_2(P_{R_2N_2}) > N_2^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} > 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_{2,l}, d_2^*]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$. (iii) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$.
- (g) Assume $\partial N_1^*/\partial d_2 < 0$ and $\partial N_2^*/\partial d_2 > 0$ at P_4 . (i) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_2^*) > N_1^*(P_4)$. Otherwise, $\bar{N}_1(P_{R_1N_1}) > N_1^*(P_4)$. (ii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} > 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_2^*, d_{2,h}]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) > N_2^*(P_4)$. If $P_{3,N_2}(d_2)$ has non-positive entries for some $d_2 \in [d_2^*, d_{2,h}]$, then $\bar{N}_2(P_{R_2N_2}) > N_2^*(P_4)$.
- (h) Assume $\partial N_1^*/\partial d_2 < 0$ and $\partial N_2^*/\partial d_2 < 0$ at P_4 . (i) $\bar{N}_1(P_{R_1N_1}) > N_1^*(P_4)$. (ii) If $P_{3,N_1}(d_1^*)$ has positive entries, then $\hat{N}_1(P_{3,N_1}, d_1^*) < N_1^*(P_4)$. (iii) If $\Delta\bar{\Delta}(1 - \alpha^2)/\bar{\delta} < 0$ and $P_{3,N_2}(d_2)$ has positive entries for $d_2 \in [d_2^*, d_{2,h}]$, then $\hat{N}_2(P_{3,N_2}, d_2^*) < N_2^*(P_4)$.

Proof. Due to the similarities of the proofs, we will only prove (a) from theorem 1. To help with presentation of the proof, we redefine the notation for P_4 . Let $P_4(d_1, d_2) = [R_1^*(d_1, d_2), R_2^*(d_1, d_2), N_1^*(d_1, d_2), N_2^*(d_1, d_2)]$ denote the coexistence equilibrium where all parameters except d_1 and d_2 are fixed at p^* . The coexistence equilibrium for p^* is denoted by $P_4(d_1^*, d_2^*)$. Assume $\bar{\Delta} > 0$, $\partial N_1/\partial d_1 < 0$, and $\partial N_2/\partial d_1 > 0$. Differentiating the R_1 and R_2 entries of P_4 yields

$$\begin{aligned} \frac{\partial R_1^*}{\partial d_1} &= -b_{22}c_{22}/\bar{\Delta}; & \frac{\partial R_2^*}{\partial d_1} &= b_{21}c_{21}/\bar{\Delta}; \\ \frac{\partial R_2^*}{\partial d_2} &= -b_{11}c_{11}/\bar{\Delta}; & \frac{\partial R_1^*}{\partial d_2} &= b_{12}c_{12}/\bar{\Delta}. \end{aligned} \tag{E1}$$

Note that $\bar{\Delta} > 0$ implies $\partial R_i^*/\partial d_i > 0$ and $\partial R_i^*/\partial d_j > 0$ for $i \neq j$.

Proof of a(i): Because $\partial R_1^*/\partial d_1 < 0$, $\partial N_1^*/\partial d_1 < 0$, and $\partial N_2^*/\partial d_1 > 0$, as the value of d_1 is increased from d_1^* to d_1, h , one of following must occur: (i) $N_1^*(d_{1,h}, d_2^*) = 0$ and $R_1^*(d_{1,h}, d_2^*) > 0$ or (ii) $R_1^*(d, d_2^*) = 0$ for some $d \in (d_1^*, d_{1,h})$.

We first show that the second case occurs if and only if $P_{3,N_2}(d_2^*)$ has positive entries. Assume $N_1^*(d_{1,h}, d_2^*) = 0$ and $R_1^*(d_{1,h}) > 0$. Because $d_{1,h} > d_1^*$, $\partial R_2^*/\partial d_1 > 0$, $\partial N_2^*/\partial d_1 > 0$, and $R_1^*(d_{1,h}) > 0$, it must be the case that $P_4(d_{1,h}, d_2^*)$ has exactly one non-positive entry, namely $N_1^*(d_{1,h}, d_2^*) = 0$. Note that $P_4(d_{1,h}, d_2^*)$ and $P_{3,N_2}(d_2^*)$ are the same point. Hence, $P_{3,N_2}(d_2^*)$ must exist and have positive entries. Conversely, assume $P_{3,N_2}(d_2^*)$ has positive entries. Since $P_4(d_1^*, d_2^*)$ exists and system (1) is a Lotka-Volterra system, there must exist a value $d_{1,h}$ such that N_1 can invade for $d_1 < d_{1,h}$ and N_1 cannot invade for larger values of $d_1 > d_{1,h}$. At $d_1 = d_{1,h}$, $N_1^*(d_{1,h}, d_2^*) = 0$ and the equilibria $P_4(d_{1,h}, d_2^*)$ and $P_{3,N_2}(d_2^*)$ are the same point. Hence, $N_1^*(d_{1,h}, d_2^*) = 0$ and $R_1^*(d_{1,h}, d_2^*) > 0$.

Assume $P_{3,N_2}(d_2^*)$ has positive entries. Because $N_1^*(d_{1,h}, d_2^*) = 0$, $R_1^*(d_{1,h}, d_2^*) > 0$, $\partial R_2^*/\partial d_1 > 0$ and $\partial N_2^*/\partial d_1 > 0$, we have that $N_2^*(d_1^*, d_2^*) < N_2^*(d_{1,h}, d_2^*) = \hat{N}_2(P_{3,N_2}, d_2^*)$. Alternatively, assume $R_1^*(d, d_2^*) = 0$ for $d_1^* < d < d_{1,h}$. When $d_1 = d$, the coexistence equilibrium satisfies

$$\begin{aligned} R_2^*(d, d_2^*) &= \frac{d_2}{b_{22}c_{22}} = \frac{d}{b_{12}c_{12}} \\ N_1^*(d, d_2^*) &= \frac{1}{c_{12}}[r_2 - k_2 R_2^*(d, d_2^*)] - \frac{c_{22}}{c_{12}} N_2^*(d, d_2^*) \\ N_2^*(d, d_2^*) &= \frac{1}{c_{22}}[r_2 - k_2 R_2^*(d, d_2^*)] - \frac{c_{12}}{c_{22}} N_1^*(d, d_2^*) \end{aligned} \quad (E2)$$

Note that setting $N_1(d, d_2^*) = 0$ in the above yields the boundary equilibrium $P_{R_2 N_2}$. Thus, because $\partial N_2^*/\partial d_1 > 0$ and $d > d_1^*$, we have that $\bar{N}_2(P_{R_2 N_2}) \geq N_2^*(d, d_2^*) > N_2^*(d_1^*, d_2^*)$.

Proof of a(ii): Assume $\Delta\bar{\Delta}(1 - \alpha^2)/\delta < 0$. Because $\partial R_1^*/\partial d_1 < 0$, $\partial R_1^*/\partial d_1 > 0$, $\partial N_1^*/\partial d_1 < 0$, and $\partial N_2^*/\partial d_1 > 0$, as the value of d_1 is decreased from d_1^* to $d_{1,l}$, one of following must occur: (i) $N_2^*(d_{1,l}, d_2^*) = 0$ and $R_2^*(d_{1,l}, d_2^*) > 0$ or (ii) $R_2^*(d, d_2^*) = 0$ for some $d \in (d_{1,l}, d_1^*)$. Similar to the proof of a(i), the former occurs if and only if $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$.

Assume $P_{3,N_1}(d_1)$ has positive entries for $d_1 \in [d_{1,l}, d_1^*]$. Because $N_2^*(d_{1,l}, d_2^*) = 0$, $R_1^*(d_{1,l}, d_2^*) > 0$, $R_2^*(d_{1,l}, d_2^*) > 0$ and $\partial N_1^*/\partial d_1 < 0$, we have that $N_1^*(d_1^*, d_2^*) < N_1^*(d_{1,l}, d_2^*) = \hat{N}_1(P_{3,N_2}, d_{1,l})$. Because $\hat{N}_1(P_{3,N_2}, d_1)$ is an increasing function of d_1 when $\Delta\bar{\Delta}(1 - \alpha^2)/\delta < 0$, we have $N_1^*(d_1^*, d_2^*) < N_1^*(d_{1,l}, d_2^*) = \hat{N}_1(P_{3,N_2}, d_{1,l}) < \hat{N}_1(P_{3,N_2}, d_1^*)$. \square

Appendix E.3 Extinction sequences induced via increased mortality

The proofs of the theorems in the previous section are based on the sequences of extinctions that occur via large increases or decreases in predator mortality. Here, we use that theory to explore some of the nonintuitive effects that arise via large increases in mortality.

Throughout we focus on increases in the mortality rate of one predator. We denote the perturbed predator by N_j and the unperturbed predator by N_k . As the mortality rate d_j is increased, eventually one prey or predator species will go extinct. Which particular species goes extinct first is determined by the relative abundances of the species at the coexistence equilibrium, the derivatives (C1) through (C4), and the analogous derivatives of the prey equilibrium densities (equations (E1) in the proof theorem 5). There are three possibilities: (1) the perturbed species (N_j) goes extinct first, (2) one of the prey species (R_1 or R_2) goes extinct first, or (3) the unperturbed predator (N_k) goes extinct first. Subsequent extinctions may occur as d_j is increased further. In the following we list the sequences of extinctions that occur as d_j increases. Note that we do not consider cases where one predator species cannot exist in the absence of the second predator; see next subsection.

Case 1: Perturbed predator (N_j) extinction occurs first. In this case, the perturbed predator goes extinct first as its mortality is increased. When the perturbed predator goes extinct, one of the prey species may also go extinct via competitive exclusion or apparent competition. After the perturbed predator goes extinct, no further changes in equilibrium densities occur as d_j is increased. Mathematically, after the perturbed predator goes extinct, the system will converge to one of the allopatric equilibria of the unperturbed predator (P_{R_1, N_k} , P_{R_2, N_k} , or P_{3, N_k}). A necessary condition for this case to occur as d_j increases is $\partial N_j^* / \partial d_j < 0$, i.e., the perturbed predator does not exhibit a hydra effect.

Case 2: Prey extinction occurs first. In this case, one of the two prey species goes extinct first. When that prey species goes extinct, it causes the perturbed predator to also go extinct. Thus, only the other prey species and the unperturbed predator remain. Further increases in d_j do not affect the system. Note that mathematically, the two predator species can coexist with the remaining prey species at the bifurcation point where the first prey species goes extinct. However, for our Lotka-Volterra model this coexistence is structurally unstable because any infinitesimal increase in d_j will cause the perturbed predator to go extinct.

Case 3: Unperturbed predator (N_k) extinction occurs first. In this case, increases in the mortality rate of the perturbed predator (d_j) cause the unperturbed predator to go extinct first. If the perturbed species does not exhibit a hydra effect, then the perturbed predator will coexist with both prey species after the unperturbed predator goes extinct. Alternatively, if the perturbed species does exhibit a hydra effect, then the perturbed predator will coexist with only one prey species after the

unperturbed predator goes extinct. In either case, further increases in the perturbed predator's mortality rate will eventually drive the perturbed predator to extinction. Extinction of the perturbed predator allows for the unperturbed predator to invade the system and coexist with one or both prey species. Further increases in d_j do not affect the system. A numerical example illustrating the extinction sequence that occurs when the perturbed predator exhibits a hydra effect is presented in Figure 6A of the main text.

Mathematically, a transcritical bifurcation occurs between P_4 and P_{3,N_j} when the unperturbed predator (N_k) goes extinct. As discussed in appendix B, P_{3,N_j} is a saddle point equilibrium when N_j exhibits a hydra effect in the full system and is stable otherwise. Thus, if N_j exhibits a hydra effect in the full system, then the system will converge to either P_{R_1,N_j} or P_{R_2,N_j} . Note that for $\alpha < 1$, N_j cannot exhibit a hydra effect in the three-species subsystem (for $\alpha < 1$). Thus, further increases in d_j drive the equilibrium density of N_j to zero, which then allows for the invasion of N_k .

Appendix E.4 Existence dependent on coexistence

In some regions of parameter space, one predator cannot coexist with either prey in the absence of the other predator. As noted in the main text, in these cases there is always at least one positive indirect effect when using comparisons of allopatric and sympatric densities (method 3). Below we present the mathematical conditions for when N_1 cannot exist in the absence of N_2 and vice versa. Note that the following cannot occur under traditional resource partitioning.

N_1 cannot exist in the absence of N_2 : This occurs when P_4 exists and in the R_1, R_2, N_1 -subspace (i) the $P_{R_2 N_1}$ equilibrium can be invaded by R_1 and (ii) the equilibrium point with only R_1 present $(r_1/k_1, 0, 0, 0)$ cannot be invaded by R_2 or N_1 . Note that together these conditions imply that $P_{R_1 N_1}$ and P_{3, N_1} do not exist in the positive orthant. The conditions on the parameters are $b_{11}c_{11}r_1/k_1 - d_1 < 0$, $b_{12}c_{12}r_2/k_2 - d_1 > 0$, $\alpha/q > k_1r_2/k_2r_1$, $\alpha q < k_2r_1/k_1r_2$, $\alpha < 1$ and

$$0 < \frac{\partial \dot{R}_1}{\partial R_1}(P_{R_2 N_1}) = r_1 \left(1 - \frac{d_1 k_1}{b_{12} c_{12} r_1} \alpha q \right) - \frac{c_{11} r_2}{c_{12}} \left(1 - \frac{d_1 k_2}{b_{12} c_{12} r_2} \right) \quad (\text{E3})$$

Since we need $0 < \frac{\partial \dot{R}_1}{\partial R_1}(P_{R_2 N_1})$, this phenomenon can only occur under defense-based partitioning when N_1 is more sensitive to prey defense ($\Delta > 0$).

For the special case where N_1 cannot attack the more defended prey ($c_{11} = 0$), the above conditions simplify to $c_{11} = b_{11}c_{11} = 0$, $b_{12}c_{12}r_2/k_2 - d_1 > 0$, $\alpha/q > k_1r_2/k_2r_1$, $\alpha q < k_2r_1/k_1r_2$, and $\alpha < 1$. A particular parameter set satisfying these conditions is

$$\begin{aligned} r_1 = k_1 = 0.5; r_2 = k_2 = 0.6; c_{11} = 0; c_{12} = 1.5; c_{21} = 1.7; c_{22} = 1.8; \\ d_1 = 0.54; d_2 = 0.8; \alpha = 0.98; q = 0.97 \end{aligned} \quad (\text{E4})$$

The result also holds for $c_{11} < d_1$.

N_2 **cannot exist in the absence of N_1** : This occurs when P_4 exists and in the R_1, R_2, N_2 -subspace (i) the $P_{R_2N_2}$ equilibrium can be invaded by R_1 and (ii) the equilibrium point $(r_1/k_1, 0, 0, 0)$ cannot be invaded by R_2 or N_2 . Note that together these conditions imply that $P_{R_1N_2}$ and P_{3,N_2} do not exist in the positive orthant. The conditions on the parameters are $b_{21}c_{21}r_1/k_1 - d_2 < 0$, $\alpha/q > k_1r_2/k_2r_1$, $\alpha q < k_2r_1/k_1r_2$, $\alpha < 1$, and

$$0 < \frac{\partial \dot{R}_1}{\partial R_1}(P_{R_2N_2}) = r_1 \left(1 - \frac{d_2 \alpha q k_1}{b_{22} c_{22} r_1} \right) - \frac{c_{21} r_2}{c_{22}} \left(1 - \frac{d_2 k_2}{b_{22} c_{22} r_2} \right). \quad (\text{E5})$$

Under the above conditions, $(r_1/k_1, 0, 0, 0)$ is the only stable equilibrium in the R_1, R_2, N_2 -subspace. This phenomenon only occurs under defense-based partitioning when N_2 is more sensitive to prey defense ($\Delta < 0$).

For the special case where N_2 cannot attack the more defended prey ($c_{21} = 0$), the above conditions simplify to $c_{21} = b_{21}c_{21} = 0$, $b_{22}c_{22}r_2/k_2 - d_2 > 0$, $\alpha/q > k_1r_2/k_2r_1$, $\alpha q < k_2r_1/k_1r_2$, and $\alpha^2 < 1$. A particular numerical example is

$$\begin{aligned} r_1 = k_1 = 1.2; r_2 = k_2 = 3; c_{11} = 0.54; c_{12} = 1; c_{21} = 0; c_{22} = 2.4; \\ d_1 = 0.44; d_2 = 0.7; \alpha = 0.94; q = 0.85 \end{aligned} \quad (\text{E6})$$

The result also holds for positive c_{21} , provided $c_{21} \leq 0.67$.