INTERFERENCE COMPETITION ON GROUP DEFENSE WITH HOLLING TYPE IV COMPETITIVE RESPONSE

Marcos Marva
marcos.marva@uah.es

Hamlet Castillo Alvino
hamlet.castillo@ce.pucmm.edu.do

Department of Physics and Mathematics
University of Alcala
Madrid, Spain

Content

Introduction: Brief context and novelties

Species competition is present under many different forms and strategies including aggressiveness [Balance,2001], [DOW,1977]. In particular, group defense has been observed among these mechanisms [Miller,1922] [Krause,2002] for both vertebrate or invertebrate animals.

Left picture: An Argentine ant Linepithema humile Vs Pogonomyrmex californicus. Photo by Dr. Dong-Hwan Choe [Welzel,2018](see also [Barton,2002] case of experimental interference competition on group defense). **Right picture**:Humpback whales (Megaptera novaeangliae) Vs killer whales (Orcinus orca) [Pitman,2016].

Introduction: Brief context and novelties

No.	Functional response exhibiting group defense	Authors	Model
(1-a)	$f(x) = \dfrac{mx}{a_0 + a_1 + a_2x^2}$	[Andrew,1968]	Enzymatic reaction model (Mono-Haldane Functional)
(1-b)	$f(x) = \dfrac{x}{m + bx^2}$	[Sugui,Howell,1980]	*Predator-prey model*,simplified (Mono-Haldane Functional)
(2)	(1-a)	[Freedman,1986]	*Predator-prey model*, mutual interference among predators
(3)	$f(x) = \dfrac{x}{m + bx^2}$	[Raw,2017]	*Predator-prey model* with one prey and two Predator
(4)	$a\sqrt{x}$	[Ajraldi,2011] [Venturino,2011] [Banerjee,2018]	Square Root functional functional Response term

Table: Chronology of the group defense in predator-prey models with Holling type IV term functional response. See also [Xiao,2001], [Mezzalira,2017] although the authors do not use differential equations.

Departure model and reformulation

Some assumptions formulations about of functional response in predator-prey models, can be derive assuming:

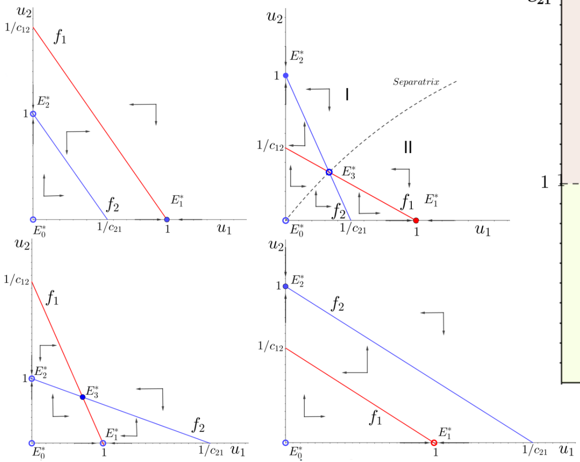
1. The *handling time* is linearly increasing with respect to N (the total amount of preys).
2. Where the functional response is derived by assuming both a linearly increasing handling time and an inverse-linear attack rate [Colling,1997].

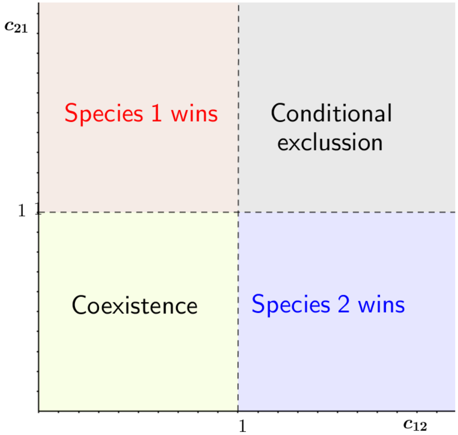
The classical interference competition model [Braun,1983] (see also [Arrowsmith,1992])

$$\begin{cases} x_1' = r_1x_1 - a_{11}x_1^2 - f_1(x_1)x_2 \\ x_2' = r_2x_2 - a_{22}x_2^2 - f_2(x_2)x_1 \end{cases} \tag{1}$$

Where $f_i(x_i) = a_{ij}x_i, \quad i,j = 1,2,$ (Holling Type I Functional Response).

Left panel: possible phase portrait of the classical model (1). Right panel: competition outcomes as function of the competitive strength c_{12} and c_{21}.





Departure model and reformulation

The basic assumption of the classical model is that the *per capita* growth rate of species i decreases linearly with x_i and x_j $(i \neq j)$

$$\frac{x_i'}{x_i} = r_i - a_{ii}x_i - a_{ij}x_j, \qquad i \neq j, \qquad i,j = 1,2$$

An alternative formulation that, essentially, is an adaptation of [Koen,2007] to the current context. The first part of the exposition follows [Marva,Castillo,2019]: as in [Holling,1959b], we assume that

$$N_i = aT_{actv}x_i, \quad T = T_{actv} + T_{int}N_i$$

where x_i is the total amount of individuals of species i, T_{actv} stands for the time that individuals are active (searching for resources or territories, matching,. . .), a is a constant equivalent to Holling's discovery rate. But, if $T > T_{actv}$, then $T_{actv} = T - T_{int}N_i$, that implies $N_i = aT_{actv}x_i = a(T - T_{int}N_i)x_i$ that is equivalent to $N_i = \dfrac{aTx_i}{1 + aT_{int}x_i}$ that we called *Holling type II competitive response to interference time* in [Marva,Castillo,2019].

We assume now that the interference time is not constant; instead, it increases linearly with the number of individuals of species i

$$T_{int} \equiv (b + dx_i)T_{intx}$$

which modelizes group defense; therefore

$$N_i = \frac{aTx_i}{1 + T_{intx}abx_i + T_{intx}adx_i^2},$$

We call Holling type IV *competitive response to interference time on group defense*. Note that either b or d equal zero, so that $d = 0$ means that assembling individuals of species 1 has no effect while $b = 0$ means that group defense is a common feature in species 1. Plugging this expression in system (1) and relabeling coefficients yields

$$\frac{x_i'}{x_i} = r_i - a_{ii}x_i - \frac{a_{ij}x_j}{1 + a_i x_i^2}, \qquad i \neq j, \qquad i, j = 1, 2, \tag{2}$$

where $a_i = adT_{intx}$. Thus, the inter-species competition rate is constant only if interactions are instantaneous (i.e., $T_{int} = 0$). In other case, the effect of species j on species i is density dependent, a decreasing function of x_i^2 for a fixed amount of individuals of species j.

Competitive response to interference time on group defense

Can be interpreted as the ability of a group individuals of the species i to reduce the inter species competition impact when species i population size becomes larger than species j population size $(i \neq j)$. Provided that $u_i = a_{ii}x_i/r_i$, $c_{ij} = a_{ij}/(r_i a_{ii})$ and $c_i = a_i/a_{ii}$. The system (1) we can rewrite (1).

$$\begin{cases} u_1' = r_1 \left(u_1 - u_1^2 - \dfrac{c_{12}u_1u_2}{1 + c_1u_1^2} \right) \\ u_2' = r_2 \left(u_2 - u_2^2 - \dfrac{c_{21}u_2u_1}{1 + c_2u_2^2} \right) \end{cases} \tag{3}$$

Holling type IV Competitive response to interference time on group defense

Theorem

Consider system (3). Then,

1. *The axes are forward invariant.*
2. *The solutions are bounded from above.*
3. *The positive cone is forward invariant.*

Theorem

Consider system (3). Then,

1. *The trivial equilibrium point $E_0^* = (0,0)$ is unstable (note that $r_i > 0$).*
2. *There exist semitrivial equilibrium points $E_1^* = (1,0)$ and $E_2^* = (0,1)$. Besides:*
   - (i) E_i^* *is globally asymptotically stable if* $c_{ji} < 1$, $i \neq j$.
   - (ii) E_i^* *is unstable stable if* $c_{ji} > 1$, $i \neq j$.

Holling type IV Competitive response to interference time on group defense on just one species

Aimed to gain an insight on the role of the functional response, we first assume that only species 1 has the ability of reduce the effect of species when increasing the number of individuals of species 1. As the following system is a particular case of system (3), is well behaved.

$$\begin{cases} u_1' = r_1 \left(u_1 - u_1^2 - \dfrac{c_{12} u_1 u_2}{1 + c_1 u_1^2} \right) \\ u_2' = r_2 (u_2 - u_2^2 - c_{21} u_1 u_2) \end{cases} \tag{4}$$

Holling type IV Competitive response to interference time on group defense on just one species

We focus on the nontrivial equilibrium points. The coexistence equilibrium $E^*_{\pm}$ of system (4) arises from the roots of the equation:

$$P(u_1) = u_1^3 - u_1^2 + \frac{s}{c_1}u_1 - \frac{r}{c_1}$$

where, $r = 1 - c_{12} \quad and \quad s = 1 - c_{12}c_{21}$, applying the Sturm's theorem we obtain the strum's sequence

$$Seq_p = \{P(u_1), P'(u_1), R_1(u_1), R_2(u_1)\}$$

and analyzing the sign of the term $R_2(u_1)$ yields the threshold values

$$c^*_{1\pm} = \frac{27r^2 - 18sr - s^2 \pm \sqrt{(r-s)(9r-s)^3}}{8r} \tag{5}$$

Holling type IV Competitive response to interference time on group defense on just one species

Theorem (Coexistence)

Consider system (4) and assume that $0 < c_{ij} < 1$, $i,j = 1,2$ *with* $c_1 > 0$. *Consider also the quantities* (5)*vThen, for any solution with initial values in the positive cone:*

1. *There exist three equilibrium points* E_+^*, E_-^* *and* E^* *in the positive cone if* $c_1 \in (c_{1-}^*, c_{1+}^*)$, *where* $c_{1\pm}^*$ *were defined in (5). In such a case, exist a nontrivial equilibrium point* E_+^* *unstable while* E^* *and* E_-^* *are locally asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through* E_+^*.
2. *The equilibrium point* E^* *is globally asymptotically stable if* $c_1 \in (0, c_{1-}^*) \cup (c_{1+}^*, \infty)$.

Holling type IV Competitive response to interference time on group defense on just one species

Theorem (bi-stable conditional coexistence)

consider system (4) and assume that $c_{12} > 1$, $0 < c_{21} < 1$ *and* $c_1 > 0$. *Then, for any solution with initial values in the positive cone:*

1. *There exist two nontrivial equilibrium points* E_+^* *and* E_-^* *in the positive cone if* $c_1 \in (c_{1-}^*, \infty)$, *where* c_{1-}^* *was defined in (5). In such a case, the nontrivial equilibrium point* E_-^* *defined in theorem 6 is unstable while the semi-trivial* E_2^* *and nontrivial* E_+^* *are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through* E_-^*.
2. *The semi-trivial equilibrium point* E_2^* *is globally asymptotically stable if* $c_1 \in (0, c_{1-}^*)$.*In such a case, the semi-trivial equilibrium point* E_1^* *is unstable.*

Holling type IV Competitive response to interference time on group defense on just one species

Theorem (species 1 wins)

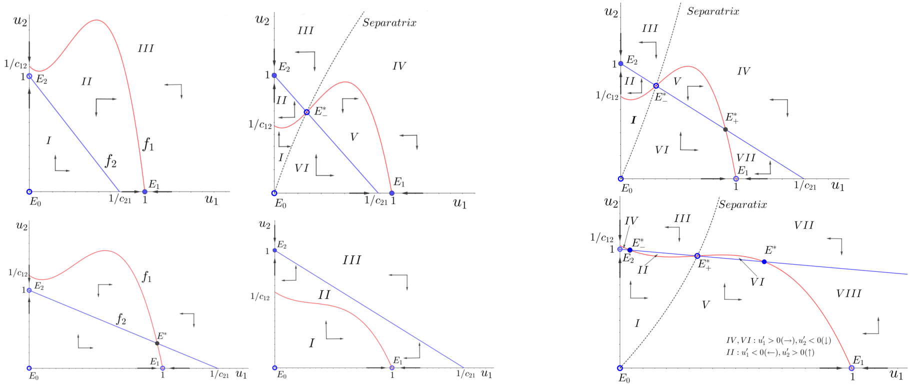
Consider system (4) with $c_1 > 0$. Then, for any solution with initial values in the positive cone, E_1^* is globally asymptotically stable if $c_{21} > 1$ and $0 < c_{12} < 1$.

Theorem (conditional exclusion.)

Consider system (4) and assume that $c_{ij} > 1 \quad i, j = 1, 2$ and $c_1 > 0$. Then, there exist a equilibrium point E_-^* that is unstable while E_1^* and E_2^* (defined in theorem 2) are asymptotically stable, each of which has a basin of attraction defined by a separatrix passing through E_-^*.

Holling type IV Competitive response to interference time on group defense on just one species

The following result displays conditions that describe those scenarios such that the asymptotic behavior of the solutions of system (4) is the same as in system (2).



Holling type IV Competitive response to interference time on group defense on just one species

Theorem	Competition outcomes	$c_{ij}, i, j = 1, 2$ values	c_1 values
3	Bi-stable unconditional	$0 < c_{ij} < 1$	$c_1 \in (c^*_{1-}, c^*_{1+})$
	and classical coexistence		$c_1 \in (0, c^*_{1-})$ $c_1 \in (c^*_{1+}, \infty)$
4	Bi-stable Conditional coexistence	$c_{12} > 1 \quad 0 < c_{21} < 1$	$c_1 \in (c^*_{1-}, \infty)$
	or Species 2 wins		$c_1 \in (0, c^*_{1-})$
5	Species 1 Wins	$c_{21} > 1 \quad 0 < c_{12} < 1$	$c_{1\pm}$ fails
6	Conditional Exclusion	$c_{ij} > 1$	$c_{1\pm}$ fails

Table: Conditions competitive strength c_{ij} and group defense coefficient c_i for the existence of nontrivial equilibrium points of the system (4) in the positive cone under the behavior of symmetric competition that correspond for the different biologically competition scenarios.

Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)

we focus on the existence and stability of the nontrivial equilibrium points. The nullclines of system (3) are third degree equations, defined by

$$u_2 = f_1(u_1) = (1-u_1)(1+c_1u_1^2)/c_{12}, \qquad u_1 = f_2(u_2) = (1-u_2)(1+c_2u_2^2)/c_{21} \quad (6)$$

so that the equilibrium points are given by the solutions to the ninth degree equation

$$P(u_1) = \frac{1}{c_{12}^3 c_{21}} \sum_{k=0}^{9} \gamma_k u^k \quad (7)$$

we define the parameters of competitive strength and group defense coefficient as $c_{12} = c_{21} \equiv \hat{c}$ and $c_1 = c_2 \equiv c$. In such a case, equation (7) can be written as follow:

$$P(u_1) = \frac{1}{\hat{c}^4} g(u_1)h(u_1), \quad (8)$$

Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)

where,

$$g(u_1) = cu_1^3 - cu_1^2 + (1+\hat{c})u_1 - 1$$

and

$$\begin{aligned} h(u_1) = \quad & c^3u_1^6 - 2c^3u_1^5 + \left[c^3 + c^2(2-\hat{c})\right]u_1^4 \\ & -2c^2(2-\hat{c})u_1^3 + \left[c^2(2-\hat{c}+c(\hat{c}^2)-\hat{c}+1)\right]u_1^2 \\ & +(-c\hat{c}^2 + 2c\hat{c} - 2c)u_1 + (c + \hat{c}^2 - c\hat{c} - \hat{c}^3) \end{aligned}$$

we considered the nullclines (6) under symmetric competition. Applying Sturm's theorem we obtain the sturm's sequence of the polinomial (8):

$$Seq_g = \{g(u_1), g'(u_1), R_1(u_1), R_2(u_1)\}$$

$$Seq_h = \{h(u_1), h'(u_1), T_1(u_1), T_2(u_1), T_3(u_1), T_4(u_1), T_5(u_1)\}$$

Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)

these sequences are calculated as in theorem 5. Analyzing the terms of the above sequences $R_2(u_1)$,$T_4(u_1)$,$T_5(u_1)$ we found the sign of the above terms yields the thresholds values

$$\begin{aligned} c^*_{\pm} &= \frac{\hat{c}^2+20\hat{c}-8\pm\sqrt{\hat{c}(\hat{c}-8)^3}}{8} \\ c^{**}_{\pm} &= \frac{-3\hat{c}^2+20\hat{c}-8\pm\sqrt{\hat{c}(9\hat{c}-8)(\hat{c}+8)^2}}{8} \\ c^{***} &= -\frac{13\hat{c}^2+\sqrt{-\hat{c}(7\hat{c}-8)^3}-4\hat{c}-8}{8(\hat{c}-1)} \end{aligned} \tag{9}$$

which give us the sign variation for the existence of one,three or five real roots as shown in the following table.

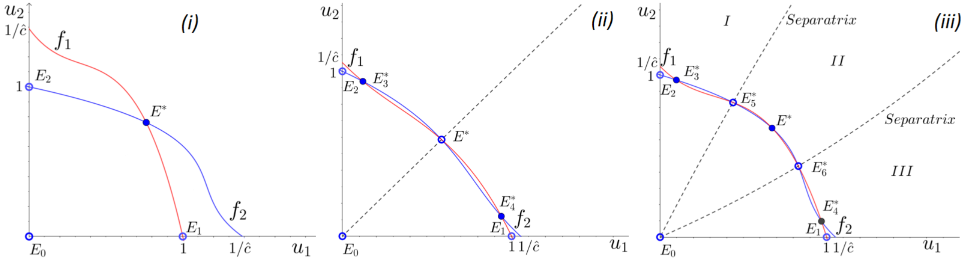
Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)

Theorem	Competition outcomes	$\hat{c}$ values	c values
6.1	Classical coexistence	$\hat{c} \in (0,1)$	$c \in (0, c_+^{**})$ $c \in (c^{***}, \infty)$
6.2	Multi-stability	$\hat{c} \in \left(\frac{8}{9}, 1\right)$	$c \in (c_+^{**}, c_-^{**})$ $c \in (c_+^{*}, c^{***})$
6.3	Classical exclusion	$\hat{c} \in (1, \infty)$	$c \in (0, c_+^{**})$
6.4	Conditional coexistence	$\hat{c} \in (1, \infty)$	$c \in (c_+^{**}, \infty)$

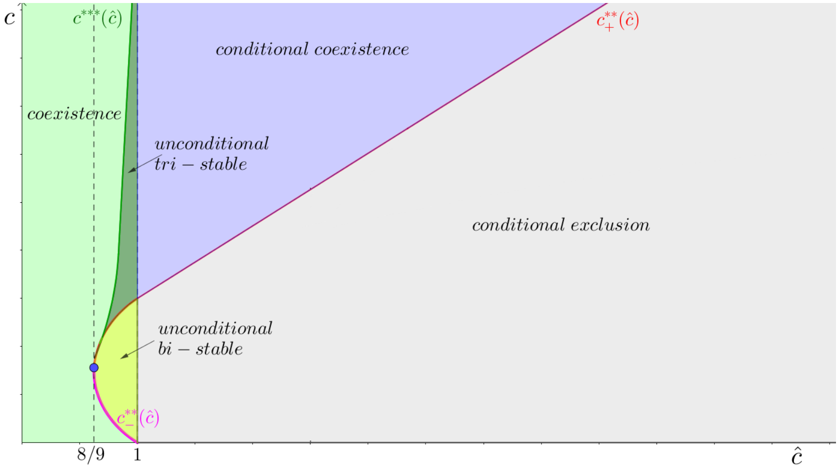
Table: Conditions $\hat{c}$ and c for the existence of nontrivial equilibrium points of the system (3) in the positive cone under the behavior of symmetric competition that correspond for the different biologically competition scenarios.

Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)

The following result displays new scenarios phase portrait



Holling type IV Competitive response to interference time on group defense on both species (symmetric competition)



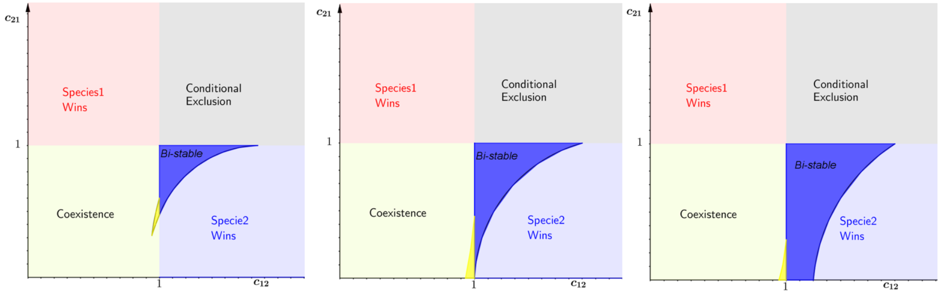


Figure: Competition outcomes of system (4) as function of competitive strengths c_{12},c_{21} for increasing values of c_1 (from left to right). The color is de same as in classical model figure 6 except the dark blue and yellow regions that represents bi-stable conditional coexistence and unconditional coexistence with two global attractor in the positive cone. The above shape is based on numerical calculations with the code source available in [castillo,2019] and has been edited to improve it.Parameter values are

$$c_{12} > 0 \quad c_{21} < 3 \quad and \quad c_1 = 1.95, 2.45, 9.$$

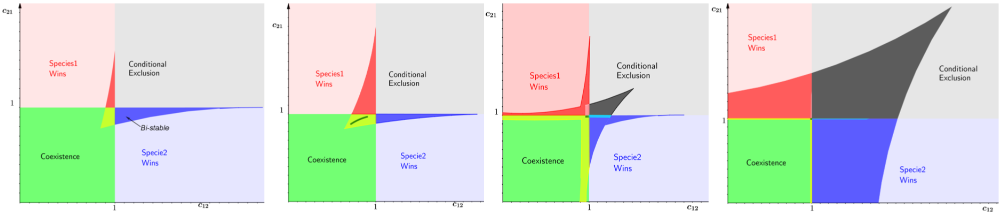


Figure: Competition outcomes of system (3) as function of competitive strengths c_{12},c_{21} for increasing values of c_1 and c_2 (from left to right). The color is de same as figure 1 except the dark blue, pink and cian color's regions that represents tri-stable conditional coexistence, the dark red region stands for bi-stable conditional coexistence region in favor species 2 and the dark-green area stands for unconditional coexistence with three nontrivial equilibrium points are globally asymptotically stable. the above shape is based on numerical calculations with the code source available in [castillo,2019] and has been edited to improve it.Parameter values are $c_{12} > 0 \quad c_{21} < 4 \quad and \quad c_1 = 1.9, 3.8, 5.8, 15; c_2 = 1.5, 4.4, 6.4, 10.$

Conclusions

1. We have found that group defense strategies improve the chances of coexistence.
2. This mechanism can be added to cooperation-competition effects [Nunney,1980] [Zhang,2003] and accounting for interfering time [Marva,Castillo,2019] as mechanisms enhancing coexistence.
3. We have found that the model proposed by [Marva,Castillo,2019] is a particular case of the model derived herein and as a consequence, the classical model too.
4. We have also found a threshold value that makes emerge the effect of group defense.
5. The resulting model expands the outcomes allowed by the classical Lotka-Volterra competition model by,
   - (i) Enlarging the range of parameter values that allow coexistence scenarios.
   - (ii) Displaying dynamical scenarios not allowed by the classical model in the form of multi-stable scenarios: bi/tri-stable conditional coexistence (species can either coexist or one/any pf them go extinct), bi/tristable unconditional coexistence (there exist two or three possible coexistence steady states).
6. The model presented herein displays stable alternative states in which the species coexist unconditionally as a result of the group defense strategy.

Next Target

Apply the new competition model to recent experimental cases and/or data as in [Barton,2002], [Mezzalira,2017], [Welzel,2018].

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Thanks for your attention!