

1 **Functional response and population dynamics for fighting predator,**  
2 **based on activity distribution**

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19 Running headline: Functional response for fighting predator

20

1 **Abstract**

2 The classical Holling type II functional response, describing the per capita predation as function  
3 of prey density, was modified by Beddington and DeAngelis to include interference of predators  
4 that increases with predator density and decreases the number of killed prey. In the present paper  
5 we further generalize the Beddington–DeAngelis functional response, considering that all  
6 predator activities (searching and handling prey, fight and recovery) have time duration, the  
7 probabilities of predator activities depend on the encounter probabilities, and hence on the prey  
8 and predator abundance, too. Under these conditions, the aim of the study is to introduce a  
9 functional response for fighting predator and analyse the corresponding dynamics, when  
10 predator-predator-prey encounters also occur.

11 From this general approach, the Holling type functional responses can be also obtained as  
12 particular cases. In terms of the activity distribution, we give biologically interpretable sufficient  
13 conditions for stable coexistence. We consider two-individual (predator-prey) and three-  
14 individual (predator-predator-prey) encounters. In the three-individual encounter model there is a  
15 relatively higher fighting rate and a lower killing rate. Using numerical simulation, we  
16 surprisingly found that when the intrinsic prey growth rate and the conversion rate are small  
17 enough, the equilibrium predator abundance is higher in the three-individual encounter case. The  
18 above means that, when the equilibrium abundance of the predator is small, coexistence appears  
19 first in the three-individual encounter model.

20 **Key-words:** activity distribution, Beddington-DeAngelis functional response, fighting between  
21 predators, population dynamics, prey-predator system

22

## 1 **1. Introduction**

2 In biological systems the interactions between individuals take time. The functional response  
3 (see e.g. Holling 1959) takes into account the handling time decreasing the number of active  
4 hunting predators. Furthermore, the abundance-dependent and time-consuming intra-specific  
5 interaction may decrease the number of hunting predators. The idea that predator abundance has  
6 an effect on **the** functional response is well-studied in ecology (e.g. Abrams 1994; Akcakaya *et*  
7 *al.* 1995; Abrams & Ginzburg 2000). From theoretical point of view, Beddington (1975) and  
8 **DeAngelis *et al.* (1975)** independently introduced a functional response that accounts for the  
9 predators' interference.

10 From experimental point of view, while e.g. Fussman *et al.* (2005) showed that consumer has an  
11 effect on the functional response only at extraordinary high abundances, e.g. **Mech (2007)** found  
12 that the best fit functional response includes predator abundance dependence.

13 In a 'paper wasp - shield beetle' system, e.g. **Schenk *et al.* (2005)** pointed out that the functional  
14 response depended on both prey and predator abundances, and both direct (e.g. aggression) and  
15 indirect (depletion of prey) interference mechanisms were at work in their system.

16 In this paper we will consider a one prey – one predator system: in the prey population there is  
17 an indirect competition (e.g. depletion of resources) and between **the** predators there is a direct  
18 interaction, i.e. when two predators encounter, they fight with each other. In this case fight does  
19 not only take time, but we can also assume that during **the** fighting occasional injury may  
20 happen, and during recovery the predators stop all other activities, including hunting (e.g. Witz  
21 1990). Furthermore, fighting also decreases the biomass of the predators (e.g. Riechert 1988).

1 Our aim is to develop a model derivation method in which two ecological phenomena can be  
2 dealt with at the same time: intra-specific competition between predators (e.g. Chase *et al.* 2002),  
3 and time duration of predator activities. If the predator can do only one activity at a time, the  
4 interference between predators and the predation process are not independent, or putting it more  
5 explicitly: Holling (1959) emphasized the importance of time constraint in predation;  
6 Beddington (1975) and DeAngelis *et al.* (1975) pointed out that the predators' interference  
7 decreases the functional response. Now we are interested in the effect of the time constraint on  
8 the competition coefficient between predators, and on the functional response simultaneously,  
9 when predator competition and predation are not independent.

10 We will start from the activity distribution of a predator. We assume that probabilities of the  
11 predator activities depend on the abundances of prey and predator populations, since the  
12 encounter probabilities do. From the activity distribution of a predator, the functional response  
13 and the number of fights per time unit can be calculated. The main point is that fighting between  
14 predators and hunting can not be handled separately, since they don't occur at the same time.

15 In Section 2 we introduce a general model for the considered situation. In Section 3, a particular  
16 class of the general model is studied: *two-individual encounter models* are considered where the  
17 focal individual cannot encounter with a prey and other predator at a time, in the same perception  
18 range. This is the consequence of the assumption that prey do not aggregate and are randomly  
19 distributed between perception ranges, and we can neglect the case when there are one prey and  
20 another predator in one perception range at the same time. The well-known *Beddington-*  
21 *DeAngelis* model is obtained as a particular case of this class. In Section 4 the case is considered  
22 when the predator abundance is large enough, so the assumption that the focal predator does not

1 encounter with a prey and a predator at the same time, is not acceptable. For simplicity, the  
2 independence of the prey and predator distributions is supposed. It is shown that these *three-*  
3 *individual encounter models* can lead to qualitatively different dynamic behaviour. In Section 5,  
4 simulation results of two- and three-individual encounter models are compared. Section 6 is  
5 dedicated to the discussion of the results. Finally, in Appendices 1-3, conditions for the  
6 coexistence and asymptotic Lyapunov stability are obtained.

7

## 8 **2. Functional response based on general predator activity distribution, the corresponding** 9 **population dynamics and stable coexistence**

10 To derive the functional response we will consider the following class of the predation processes.  
11 Predator is only locally omniscient, which has two consequences: First, the predator can observe  
12 a prey and/or a conspecific only in a given “small” area called “*perception range*”. Second,  
13 before arriving, predator has no information on a given perception range, thus it checks the  
14 perception ranges randomly. The perception ranges are classified by their contents, they may be  
15 empty, contain a prey and/or a conspecific. The distribution of different perception ranges  
16 depends on the abundance of prey and predator. We will concentrate on a short time period  $T$   
17 (for instance one day), while the change in abundances can be neglected. In other words, during  
18 time  $T$  the predators can not kill too many prey and/or other predators.

19 In summary, during the visiting process, the encounter probabilities depend on the prey and  
20 predator abundances; these encounter probabilities do not change during the time period  $T$ ; focal

1 predator finds a random series of different kind of perception ranges and all following encounter  
2 events are independent.

3 According to encounter possibilities, assume a predator has four activities. Activity 1: the  
4 predator encounters no prey and no predator. Activity 2: the predator encounters and fights with  
5 another predator (this event also includes recovery from injuries). (In a more structured model it  
6 might be included that, in case of different sizes, the smaller conspecific predator escapes.)  
7 Activity 3: the predator finds and attacks but misses a prey. Activity 4: the predator finds,  
8 attacks, kills and handles a prey. (E.g. in case of Arthropods, this event also includes capture,  
9 handling and ingestion of prey, but also the time after cleaning mouthparts, antennae and legs.) A  
10 natural assumption is that these activities rule out each other.

11 Clearly, these activities take time and have either energy (or equivalently biomass) intake, or  
12 energy loss. An observer can find the following activity distribution at fixed population  
13 abundances:

14 In Table 1 below,  $T_i$  is the average time duration of the  $i$ -th activity,  $T_S$  the searching time;  $T_F$   
15 the average “time cost” of fighting with a predator;  $T_M$  the attack time;  $T_H$  the digestion time.

16 Let  $x$  be the abundance of prey and  $y$  that of predator,  $p_i(x, y)$  denotes the probability of  $i$ -th  
17 activity. E.g.  $p_1(x, y)$  denotes the probability that the predator is searching in an empty  
18 perception range. We note that, these probabilities, apart from the abundances, may also depend  
19 on the spatial distribution of prey and predator (e.g. Kratina, Vos & Anholt 2007; Nachman,  
20 2006); on habitat complexity (e.g. Hillebrand & Cardinale 2004; Grabowski 2004) and on the  
21 behaviour of predator and/or prey.

1 Finally,  $0 < c_i$  denotes the net energy intake from the  $i$ -th activity:  $c_1$  is the cost of searching,  
2  $c_2$  the average cost of fighting activity (cost of searching plus cost of fighting),  $c_3$  the cost of the  
3 activity of missed attack (cost of searching plus cost of attack), and  $c_4$  the value of activity of  
4 successful predation (the value of prey minus the cost of searching and cost of attack).

6 Table 1

7 Now, we use the basic approach of Holling's functional response derivation (Holling 1959),  
8 namely we will calculate the average interaction rates per unit time, during a fix time duration  $T$ .  
9 We mention that optimal forager theory postulates that the forager maximizes its average net  
10 energy intake per unit time (Stephens & Krebs 1986; Turelli *et al.* 1982). Furthermore, to build  
11 up a population dynamics, we also need the time average interaction rates.

12 Now we derive the average number of predator-prey and predator-predator interactions, per unit  
13 time. These interaction rates depend on the abundances of the considered species and on the time  
14 duration of activities. We assume that during the considered time period  $T$ , the abundance of  
15 prey and that of predator do not change much. In other words, the activity distributions are  
16 constant functions of  $x$  and  $y$  within  $T$ . These assumptions allow us to use the same activity  
17 distributions during time period  $T$ , see Garay & Móri (2010). We have proved that in unit time,

18 the expected number of  $i$ -th activities can be estimated by  $\frac{p_i(x, y)}{\sum_j T_j p_j(x, y)}$ . The intuitive

19 background of this estimation is the following: During time  $T$ , we take independent samples  
20 from the given activity distribution. Since the activity distribution does not change during  $T$ , the

1 average time duration of an activity is  $\sum_j T_j p_j(x, y)$ . Thus during  $T$ , the average number of

2 activity events is  $\frac{T}{\sum_j T_j p_j(x, y)}$ . Based on independent repetitions,  $p_i(x, y)$  part of the average

3 number of activity events is the number of  $i$ -th activities. Thus during unit time, the expected

4 number of  $i$ -th activities is estimated by  $\frac{p_i(x, y)}{\sum_j T_j p_j(x, y)}$ . In particular, the functional response is

5 given by  $\frac{p_4(x, y)}{\sum_j T_j p_j(x, y)}$ , and the average number of fights during unit time is  $\frac{p_2(x, y)}{\sum_j T_j p_j(x, y)}$ .

6 Now substituting the above interaction rates into the standard ecological model (e.g. Arditi *et al.*

7 2004), **yields** the following canonical population dynamics:

$$\dot{x} = x(r_1 - ax) - \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} y$$

8 (1)

$$\dot{y} = y \left( -r_2 - \sum_{i=1}^3 \frac{c_i p_i(x, y)}{\sum_j T_j p_j(x, y)} + c_4 \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} \right),$$

9 where  $r_1$  is the intrinsic growth rate of prey,  $a/r_1$  the carrying capacity **for the prey**, and  $r_2$  the

10 intrinsic mortality rate of predator. The novelty of dynamics (1) is that in each interaction rate it

11 takes account of the time durations of all considered predator activities. **For instance, the fight**

12 **between predators is a kind of competition. In lots of dynamical models (see e.g. Haque 2011,**

13 **and the references in there) the competition coefficient does not depend on the time constraint in**

14 **the predation process. However, if the predator can do only one activity at a time and each**

15 **interaction has fixed average time duration, then the functional response and the competition**



1 coefficient are not independent, since the time constraints connect them, as we can see in  
2 dynamics (1).

#### 4 **Consistence of the model**

5 In dynamic models of ecology, a basic requirement is that the positive and nonnegative orthants  
6 are invariant and all trajectories are bounded. Each trajectory of prey is nonnegative, if  
7  $p_4(0, y) = 0$ , which always holds, since if there is no prey, then the predator cannot encounter  
8 with a prey. Furthermore, each prey trajectory is bounded, since for  $x > \frac{r_1}{a}$ , the prey density is  
9 strictly decreasing, independently of the predator density. Moreover, each predator trajectory is  
10 also nonnegative. In Appendix 1A), we have proved that, if the functional response tends to zero  
11 for predator density tending to infinity, then dynamics (1) is bounded. This condition seems  
12 natural, since when the predator density is large enough compared to the prey density, then the  
13 predator always fight. For details see Appendix 1.A).

#### 15 **Coexistence**

16 Coexistence takes place if the prey can survive, and the predator can establish a population.  
17 Firstly, the prey does not die out, if  $r_2$  is greater than the intake by the functional response when  
18 prey density is near zero. This condition seems natural, since it means that the predator cannot  
19 survive when the prey density is small enough. Secondly, as for the predator, coexistence is  
20 guaranteed by the following minimal condition: consider a stable prey population without  
21 predator, then the prey density is  $r_1/a$ . If a predator arrives in this prey population, and the former  
22 can establish a population, then coexistence occurs (for details see Appendix 1). Thirdly, if  
23 dynamics (1) is bounded and the two species coexist, then there is always an equilibrium or a

1 periodic orbit of the dynamics (1). Fourthly, we note that since in dynamics (1), the probabilities  
2 of different activities are arbitrary continuous functions, all kind of coexistence may happen:  
3 stable equilibrium or stable cycle (for details see Appendix 1).

4

### 5 **Stable equilibrium coexistence**

6 In Appendix 2, using the linearization method of stability theory, we show that the fulfilment of  
7 the following conditions (2)-(5) imply *locally stable coexistence* (i.e. local asymptotic stability of  
8 the interior equilibrium).

9 (2) At the equilibrium, the growth rate of prey resulting from the carrying capacity is less than  
10 the decay rate of **the** prey abundance by **the** predation pressure (i.e. less than the marginal rate of  
11 increase of the functional response with respect to **the** prey abundance).

12 (3) At the equilibrium the relative rate of increase of the net biomass intake with respect to **the**  
13 prey abundance is smaller than the relative rate of increase of the average time duration of an  
14 activity with respect to **the** predator abundance.

15 (4) At the equilibrium, the relative rate of decrease of the functional response with respect to the  
16 predator abundance should be large enough. The smaller the equilibrium predator abundance is,  
17 the higher this threshold is.

18 (5) At the equilibrium, the relative rate of increase of the net biomass intake with respect to  
19 the prey **abundance is greater** than the relative rate of increase of the average time duration of an  
20 activity with respect to **the** predator abundance.

21

22 In Appendix 3 we show that an appropriately defined dissipativity is a general sufficient  
23 condition for *globally stable coexistence in dynamics* (1) (i.e. for global asymptotic stability of

1 an interior equilibrium). To this end, we adapted the notion of dissipativity of a Lotka-Volterra  
2 system to our case. The term “dissipative” here is based on the fact that the interaction decreases  
3 the biomass of the system, which is a generalization of the well-known notion of dissipativity in  
4 Lotka-Volterra systems. We note that, in our case, in each interaction the biomass strictly  
5 decreases: The competition between prey and the interaction between predators has negative  
6 effect on the biomass. Furthermore, during predation the biomass of killed prey is greater than  
7 the increase in predator biomass, since there is a cost of attack and digestion as well. So, from  
8 biological view, we think system (1) is usually dissipative, but we can not proof this conjecture.

9 The consequences of the above activity distribution based modelling are illustrated with the  
10 following cases.

11

### 12 **3. Two-individual encounter model**

13 Now we consider a probabilistic model of the simplest case, when only *two-individual*  
14 *encounters* are possible, in other words, the focal predator cannot encounter with a prey and  
15 another predator at a time in the same perception range. This is implied by the assumption that  
16 prey do not aggregate and are randomly distributed between perception ranges, i.e. there is only  
17 at most one prey in each perception range. Furthermore, the abundances of prey and predator are  
18 so small that we can neglect the case when there are one prey and another predator in one  
19 perception range at the same time.

20 Suppose that the prey and predator distribution is well mixed in the home range of the predator,  
21 in a homogeneous field of  $H$  area units where the prey and predator abundances are  $x$  and  $y$ ,

1 respectively. Denote the area of a perception range of an individual predator by  $h$ , so in the  
 2 considered field there are  $\frac{H}{h}$  perception ranges. Based on the above assumptions,  $x$  and  $y$  are the  
 3 numbers of perception ranges where there is a solitary prey and a solitary predator, respectively.  
 4 Furthermore, there are  $\frac{H}{h} - x - y$  empty perception ranges. Since interactions occur only when  
 5 an individual encounters another individual, first we have to calculate the probabilities of  
 6 different encounter events.

7 In order to obtain encounter probabilities between zero and one, we have to assume that  
 8  $\frac{H}{h} \gg x + y$ . Now suppose that a focal predator individual encounters neither prey nor other

9 predator with probability  $d(0,0) = 1 - \frac{h}{H}x - \frac{h}{H}y$ , encounters a prey with probability  
 10  $d(X,0) = \frac{h}{H}x$ , and encounters another predator with probability  $d(0,Y) = \frac{h}{H}y$ . For the sake of  
 11 simplicity, here we assume that  $y \approx y-1$ . Similar assumption is widely used in random processes.

12 Now, we have to define what will happen in different encounters. Let us assume that when two  
 13 predators meet then they always fight. (Here we could suppose that the probability of fight is less  
 14 than one, but in this case we would have an extra activity: two predators encounter without  
 15 fight). Furthermore, assume that the predator is locally omniscient, i.e. in its perception range the  
 16 predator can surely observe its prey and the other predator as well, but it has no information on  
 17 the other perception ranges. Predator can kill its prey with probability  $k$ .

18 Based on the above assumption we have the following activity distribution: No interaction  
 19 happens with probability  $p_1(x, y) = 1 - p_2(x, y) - p_3(x, y) - p_4(x, y)$ , two predators fight with

1 probability  $p_2(x, y) = \frac{h}{H} y$ , predator misses a prey with probability  $p_3(x, y) = (1 - k) \frac{h}{H} x$ , and  
 2 kills it with probability  $p_4(x, y) = k \frac{h}{H} x$ . Under the present assumptions we get the activity  
 3 distribution given in Table 2.

4 Table 2

5 Now, using this actual activity distribution, we get a concrete version of population dynamics  
 6 (1):

$$7 \quad \dot{x} = x \left( (r_1 - ax) - \frac{ky}{\frac{H}{h} T_S + T_F y + [T_M + kT_H] x} \right),$$

$$8 \quad \dot{y} = y \left( -r_2 + \frac{c_4 kx - c_1 \left( \frac{H}{h} - x - y \right) - c_2 y - c_3 (1 - k)x}{\frac{H}{h} T_S + T_F y + [T_M + kT_H] x} \right).$$

9  
 10  
 11 *Beddington-DeAngelis- functional response.* Let us now ignore the cost of searching and attack,  
 12 furthermore suppose that predators fight. Moreover, assume that the predator is always  
 13 successful, i.e.  $k = 1$ , and attack does not need time,  $T_M = 0$ . In this particular case we obtain the  
 14 activity distribution given in Table 3.

15 Table 3

16

1 Hence we get back the Beddington-DeAngelis functional response, since the average number of

2 prey killed per time unit is  $\frac{x}{\frac{H}{h}T_S + T_F y + T_H x}$ . We note that our functional response derivation

3 method also gives back the classical Holling functional responses (see Garay and Móri 2011) as

4 particular cases. Dynamics (1) now reads

5

$$6 \quad \dot{x} = x \left( r_1 - ax - \frac{y}{\frac{H}{h}T_S + T_F y + T_H x} \right),$$

$$7 \quad \dot{y} = y \left( -r_2 + \frac{c_4 x - c_2 y}{\frac{H}{h}T_S + T_F y + T_H x} \right).$$

8 Here we strictly follow the steps of investigation of the general dynamics (1), but now we have a

9 concrete activity distribution.

10 Firstly, each solution is bounded if for all  $x \in ]0, \frac{r_1}{a}[$ , there exists  $y_x$ , such that for all

11  $y > y_x$  we have  $\dot{y} < 0$ , which obviously holds with  $\bar{y}_x = \frac{c_4 - r_2 T_H}{c_2 + r_2 T_F} x - \frac{r_2 T_S}{c_2 + r_2 T_F} \frac{H}{h}$ . Therefore

12 the above dynamics is bounded.

13 Secondly, the predator can establish a population, if near equilibrium  $(\frac{r_1}{a}, 0)$  of the above

14 dynamics,  $\dot{y} > 0$  holds, which is the case if

$$15 \quad r_2 < \frac{c_4 r_1}{a \frac{H}{h} T_S + T_H r_1}, \quad \dot{y} = y \left( -r_2 + \frac{c_4 x - c_2 y}{\frac{H}{h} T_S + T_F y + T_H x} \right).$$

1 Thirdly, there exists an interior equilibrium:

$$2 \quad x^* = \frac{-B + \sqrt{B^2 + 4AC}}{2A},$$

$$3 \quad y^* = \frac{c_4 - r_2 T_H}{r_2 T_F + c_2} x^* - \frac{H}{h} \frac{r_2 T_S}{r_2 T_F + c_2},$$

$$4 \quad \text{where } A = [T_F c_4 + T_H c_2] a, \quad B = \left[ \left( \frac{H}{h} T_S a - r_1 T_H \right) c_2 + (1 - r_1 T_F) c_4 - r_2 T_H \right], \quad C = \frac{H}{h} T_S [r_1 c_2 + r_2].$$

5 Local stability by linearization. The Jacobian matrix at the equilibrium is

6

$$7 \quad \mathbf{J} = \begin{pmatrix} x^* \begin{pmatrix} -a + \frac{T_H y^*}{\left( \frac{H}{h} T_S + T_F y^* + T_H x^* \right)^2} & x^* \begin{pmatrix} \frac{H}{h} T_S + T_H x^* \\ \left( \frac{H}{h} T_S + T_F y^* + T_H x^* \right)^2} \end{pmatrix} \\ y^* \begin{pmatrix} c_4 \left( \frac{H}{h} T_S + T_F y^* \right) + c_2 T_H y^* \\ \left( \frac{H}{h} T_S + T_F y^* + T_H x^* \right)^2} & y^* \begin{pmatrix} -c_2 \left( \frac{H}{h} T_S + T_H x^* \right) - c_4 T_F x^* \\ \left( \frac{H}{h} T_S + y^* + T_H x^* \right)^2} \end{pmatrix} \end{pmatrix}$$

8 Observe that the latter has the following sign structure:

$$9 \quad \mathbf{J} = \begin{pmatrix} \pm & - \\ + & - \end{pmatrix}.$$

10

11 A well-known sufficient condition for the stability of the Jacobian matrix (i.e. for the negativity

12 of the real part of each eigenvalue of  $\mathbf{J}$ ) is  $\text{tr}\mathbf{J} < 0$  and  $\text{det}\mathbf{J} > 0$ . The first inequality reads

13

14

15

16

$$\text{tr}\mathbf{J} = x^* \left( -a + \frac{T_H y^*}{\left( \frac{H}{h} T_S + T_F y^* + T_H x^* \right)^2} \right) + y^* \left( \frac{-c_2 \left( \frac{H}{h} T_S + T_H x^* \right) - c_4 x^* T_F}{\left( \frac{H}{h} T_S + y^* + T_H x^* \right)^2} \right) < 0$$

2 Observe that a sufficient condition for the latter is

$$3 \quad -a + \frac{T_H y^*}{\left( \frac{H}{h} T_S + T_F y^* + T_H x^* \right)^2} < 0.$$

4 A simple calculation shows that the latter condition also implies  $\det\mathbf{J} > 0$ , and therefore it is a  
 5 sufficient condition for the local asymptotic stability of equilibrium  $(x^*, y^*)$  for the original  
 6 nonlinear system.

7  
 8 **Numerical example 1.** We consider the parameters:  $T_S=1$ ;  $T_F=10$ ;  $T_M=2$ ;  $T_H=11$ ;  $r_1=0.7$ ;  $r_2=0.05$ ;  
 9  $a=0.01$ ;  $c_1=0.1$ ;  $c_2=0.2$ ;  $c_3=0.15$ ;  $c_4=1.4$ ;  $h=1$ ;  $H=200$ ;  $k=0.7$ . It is easy to check that both the  
 10 linearization and the Lyapunov function method (dissipativity) imply stable coexistence at  
 11 interior equilibrium  $(x^*, y^*) = (69.07, 13.31)$ , see Figure 1.

12 Figure 1

#### 14 4. Three-individual encounter model

15 When the predator abundance is large enough, our previous assumption (that the focal predator  
 16 does not encounter with prey and predator at the same time) is not reasonable (see Fussman *et al.*  
 17 2005). For the sake of simplicity, we assume that the prey and predator distributions are  
 18 independent. Thus the focal predator individual encounters a prey only, with probability



1  $d(X,0) = \frac{h}{H}x\left(1 - \frac{h}{H}y\right)$ , since the probability that one prey is in a given perception range  
2 is  $\frac{h}{H}x$ , the probability that another predator is in the same perception range, is  $x\left(1 - \frac{h}{H}y\right)$ .  
3 Furthermore, since the prey and the predator are independently distributed,  $\frac{h}{H}x\left(1 - \frac{h}{H}y\right)$  is the  
4 probability that no prey and no another predator are in a perception range. Similarly, the focal  
5 predator encounters other predator only, with probability  $d(0,Y) = \left(1 - \frac{h}{H}x\right)\frac{h}{H}y$ , encounters  
6 other predator and a prey at a time with probability  $d(X,Y) = \frac{h}{H}x\frac{h}{H}y$ , and encounters neither  
7 prey nor other predator with probability  $d(0,0) = \left(1 - \frac{h}{H}x\right)\left(1 - \frac{h}{H}y\right)$ . Moreover, assume when  
8 two predators meet, they always fight, thus the probability of fight is  
9  $p_2(x,y) = d(0,Y) + d(X,Y) = \frac{h}{H}y$ . Under these biological assumptions we get the activity  
10 distribution shown in Table 4.

11 Table 4

12 Using the actual activity distribution of Table 4, we get a concrete version of population  
13 dynamics (1):

$$\dot{x} = x(r_1 - ax) - \frac{k \frac{h}{H}x\left(1 - \frac{h}{H}y\right)}{T_S + T_F \frac{hy}{H} + T_M \frac{hx}{H} - T_M \frac{h^2xy}{H^2} + T_H \frac{khx}{H} - T_H \frac{kh^2xy}{H^2}} y,$$

16

17

1

$$\dot{y} = y \left( -r_2 + \frac{c_4 k \frac{h}{H} x \left(1 - \frac{h}{H} y\right) - c_1 \left(1 - \frac{h}{H} \left[x \left(1 - \frac{h}{H} y\right) + y\right]\right) - c_2 \frac{h}{H} y - c_3 (1-k) \frac{h}{H} x \left(1 - \frac{h}{H} y\right)}{T_S + T_F \frac{hy}{H} + T_M \frac{hx}{H} - T_M \frac{h^2 xy}{H^2} + T_H \frac{khx}{H} - T_H \frac{kh^2 xy}{H^2}} \right).$$

3 Using computer simulation, we could not find parameters for which this system had more than  
 4 one interior equilibriums. Thus we found no bistable coexistence in this system (cf. Garay *et al.*  
 5 2012).

6

7 **Numerical example 2.** If we take the parameters of Numerical example 1, for the above  
 8 dynamics we obtain that both the linearization method and the Lyapunov function method  
 9 (dissipativity) again imply stable coexistence at the interior equilibrium  $(x^*, y^*) = (69.92, 10.25)$ .

10 The system turns out to be dissipative at this equilibrium, see Figure 2.

11 

12

13

## 14 5. Comparison of the above two models

15 The fight always decreases the equilibrium abundance of predator, since the energy cost of  
 16 fighting decreases the total predator biomass, and the time duration of fighting decreases the  
 17 average number of hunting predators (in particular, during recovery predator does not hunt).

18 Consider both two-individual and three-individual encounter models at the same abundances. In  
 19 the latter we assume that two predators always fight when they encounter, no matter whether  
 20 there is a prey or not.

1 Based on this assumption, the probability of fight is the same in both models. Furthermore, the  
2 successful hunting has lower probability in the three-individual encounter model than in the two-  
3 individual one. In summary: in the three-individual encounter model there is a relatively higher  
4 fighting rate and a lower killing rate. Consequently the functional response is smaller. This  
5 means that in the three-individual encounter model the same number of predator has a smaller  
6 effect on the prey abundance than in the two-individual one.  
7 Thus, at first glance, one may expect the equilibrium predator abundance to be lower in the  
8 three-individual encounter model, since the prey surely survives in a three-individual encounter  
9 (since whenever two predators meet, they always fight). Simulations, however, show this is the  
10 case only when the conversion rate  $c_4$  is high enough (see Figure 3), and what is more, for fixed  
11  $r_1$  with growing  $c_4$ , coexistence appears first in the three-individual encounter model, and then  
12 predator abundance is higher in this model than in the two-individual encounter model, when  $c_4$   
13 is still not too large, see Figure 3.

### 14 Figure 3

15  
16 A possible explanation to this is the following: Let us consider a pair of parameters  $r_1$  and  $c_4$   
17 where there is still no coexistence in either of the two models. This means that the stably existing  
18 prey is not able to maintain the predator population. Now, for greater  $c_4$  coexistence appears first  
19 in the three-individual encounter model, where the predator is less efficient, since its functional  
20 response is lower. The latter also results in more surviving prey per unit time, therefore the  
21 higher biomass production of the prey (per unit time) may maintain the predator population.  
22 Furthermore, in this parameter range, the equilibrium predator abundance is low, having only a  
23 slight effect on killing probability.

1 For higher conversion rate (energetic value of prey)  $c_4$ , due to the higher predator abundance,  
2 fighting is more frequent in both models. Furthermore, in the three-individual encounter model,  
3 the probability of killing a prey decreases with increasing predator abundance, while in the two-  
4 individual encounter model it does not depend on **the** predator abundance. This may imply that,  
5 for high conversion rate  $c_4$ , the equilibrium predator abundance is higher in the two-individual  
6 encounter model.

7

8

## 9 **6. Discussion**

### 10 **Derivation of functional responses**

11 Over the last decades, numerous functional responses have been already introduced (see Jeschke  
12 **et al.** 2002), since there is no single functional response that would well fit to any data set (e.g.  
13 Skalski & Gilliam 2001). The main obstacle is that the functional response is very sensitive to  
14 the details of the considered biological situation. Under the assumption that during time  $T$  the  
15 abundances of interacting species do not change radically, our mechanism based method makes  
16 it possible to take into account the fine details of the considered biological case. Our method is  
17 very near the classical derivation of functional response by renewal theory (see e.g. McNamara  
18 & Houston 1999), when under the assumption that the prey population immediately renews, the  
19 functional response is also the ratio of the encounter rate and the time average. We note that the  
20 encounter distribution and the activity distribution are not the same in general, since when a  
21 predator faces an encounter situation, it may use different strategies, e.g. when predator  
22 encounters another predator then one of them may flee. In this strategic situation we obtain an

1 ecological game (see e.g. Cressman *et al.* 2014). In present paper we did not consider ecological  
2 games.

3

#### 4 **Concerning the resulting functional responses**

5 We considered the case when the predators not only hunt but also fight with each other. This is a  
6 particular case of predator interference. Based on activity distribution we also derived the  
7 Beddington-DeAngelis functional response. We note that e.g. Geritz. & Gyllenberg (2012), using  
8 differential equation at quasi-steady state, also derived a Beddington-DeAngelis type functional  
9 response, based on biological assumptions quite different from ours. While Geritz & Gyllenberg,  
10 (2012) considered non-interacting predator and prey using refuge, we considered fight between  
11 predators and prey that does not use refuge. Thus, our resulting functional responses give a slight  
12 **generalization** of the original functional responses of Beddington (1975) and DeAngelis *et al.*  
13 (1975), shedding a new light **on** them.

14

#### 15 **About stable coexistence**

16 To our knowledge, we are the first to give sufficient conditions for stable coexistence in our  
17 general model (1), based on the ecological details such as growth rate of prey **resulting** from the  
18 carrying capacity, diminishing rate of prey abundance by **the** predation pressure, rate of increase  
19 of the net biomass intake, rate of increase of the average time duration of an activity, rate of  
20 decrease of the functional response with respect to the predator abundance, rate of increase of the  
21 net biomass intake and rate of increase of the average time duration of an activity.

22 Our observation that coexistence appears first in the three-individual encounter model may have  
23 an important implication for modelling methodology. In modelling, three-individual encounters

1 (interactions) are usually neglected based on the following reasons: First, two-individual  
2 interactions are more probable. Second, higher-order encounters usually increase the non-  
3 linearity of the model, thus its analysis becomes harder. However, we have found that when the  
4 equilibrium abundance of the predator is small (thus the three-individual encounters are very  
5 improbable), coexistence appears first in the three-individual encounter model.

6 Now the question arises whether the number of encounters between predators is high  
7 enough to modify the functional response. We mention two possibilities: *First*, the territorial  
8 behaviour (and the dispersal of young predators) decreases the interaction between predators, but  
9 does not rule it out. The scanning of the territory and fighting with intruder conspecific take time  
10 (including recovery time), thus the time for predation attacks should be decreased by the predator  
11 interference, and hence the latter can increase the survival of prey. For instance, it was observed  
12 that wolves hunted little in the borders of their territory in order to avoid fatal encounters with  
13 neighbours, thus in the buffer zone of wolf packs' territories the survival rate of deer is higher  
14 (Mech 1977). Furthermore, territorial behaviour decreases the local predator abundance. Based  
15 on our observation that the predator interference ensures the coexistence with not so fecund and  
16 not so valuable prey, we think a territorial predator establishes a population easier than a non-  
17 territorial one, when their prey is not so fecund and not so valuable. *Second*, kleptoparasitism is  
18 also not an energy free and not a time free predator interference (Broom & Rychtar 2013), for  
19 which a three-individual encounter is a prerequisite. The kleptoparasitism increases the survival  
20 rate of prey, when decreases the functional response, if the time duration of kleptoparasitization  
21 is greater than searching time (thus the denominator of the functional response, i.e. the time  
22 average of one activity increases) and the encounter probability of two predators is positive (thus  
23 the numerator of the functional response, i.e. the probability to encounter only prey, decreases).

1 Although, a predator must have killed a prey before cleptoparasitization occurs, in this case the  
2 prey does surely not survive under predator interference. Furthermore, during  
3 cleptoparasitization, the predator is either injured or falls victim of a cannibal attack (Nilsson &  
4 Brönmark 1999), which also increases the predation pressure on the prey.

5 Our functional response derivation, in the future, can be applied for territorial behaviour  
6 and cleptoparasitism, but these cases need ecological game theory, since the activity of the  
7 predator becomes dependent on the strategy of the predator.

8

## 9 **Acknowledgments**

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15

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- 12

1 Table 1. General predator activity distribution.

2

<b>Activity</b>	<b>Parameter</b>	<b>Duration time</b>	<b>Probability</b>	<b>Energy</b>
Empty range found	$T_1=T_S$		$p_1(x, y)$	$-c_1$
Fight	$T_2=T_F + T_S$		$p_2(x, y)$	$-c_2$
Prey missed	$T_3=T_M + T_S$		$p_3(x, y)$	$-c_3$
Prey killed	$T_4=T_M + T_H + T_S$		$p_4(x, y)$	$c_4$

3

4

1 Table 2. Predator activity distribution in the two-individual encounter model.

<b>Activity</b>	<b>Parameter</b>	<b>Duration time</b>	<b>Probability</b>	<b>Energy</b>
Empty range found	$T_1=T_S$		$1 - [(h/H) \cdot (x + y)]$	- $c_1$
Fight	$T_2=T_F + T_S$		$(h/H) \cdot y$	- $c_2$
Prey missed	$T_3=T_M + T_S$		$(1-k) \cdot (h/H) \cdot x$	- $c_3$
Prey killed	$T_4=T_M + T_H + T_S$		$k \cdot (h/H) \cdot x$	$c_4$

2

1 Table 3. Predator activity distribution providing Beddington-DeAngelis functional response.

Activity	Parameter	Duration time	Probability	Energy
Empty range found	$T_1 = T_S$		$1 - [(h/H) \cdot (x + y)]$	0
Fight	$T_2 = T_F + T_S$		$(h/H) \cdot y$	0
Prey killed	$T_4 = T_M + T_H + T_S$		$(h/H) \cdot x$	$c_4$

2

1 Table 4. Predator activity distribution in the three-individual encounter model.

<b>Activity</b>	<b>Parameter</b>	<b>Duration time</b>	<b>Probability</b>	<b>Energy</b>
Empty range found	$T_1=T_S$		$1-(h/H) \cdot \{x \cdot [1-(h/H) \cdot y] + y\}$	$-c_1$
Fight	$T_2=T_F + T_S$		$(h/H) \cdot y$	$-c_2$
Prey missed	$T_3=T_M + T_S$		$(1-k) \cdot (h/H) \cdot x \cdot \{1-[(h/H) \cdot y]\}$	$-c_3$
Prey killed	$T_4=T_M + T_H + T_S$		$k \cdot (h/H) \cdot x \cdot \{1-[(h/H) \cdot y]\}$	$c_4$

2

1 Figure 1. Isoclines and solutions for the two-individual encounter model, with parameters of  
2 Numerical example 1. Stable coexistence at equilibrium  $(x^*, y^*)=(69.07, 13.31)$ . Programed in  
3 MatLab environment.

4

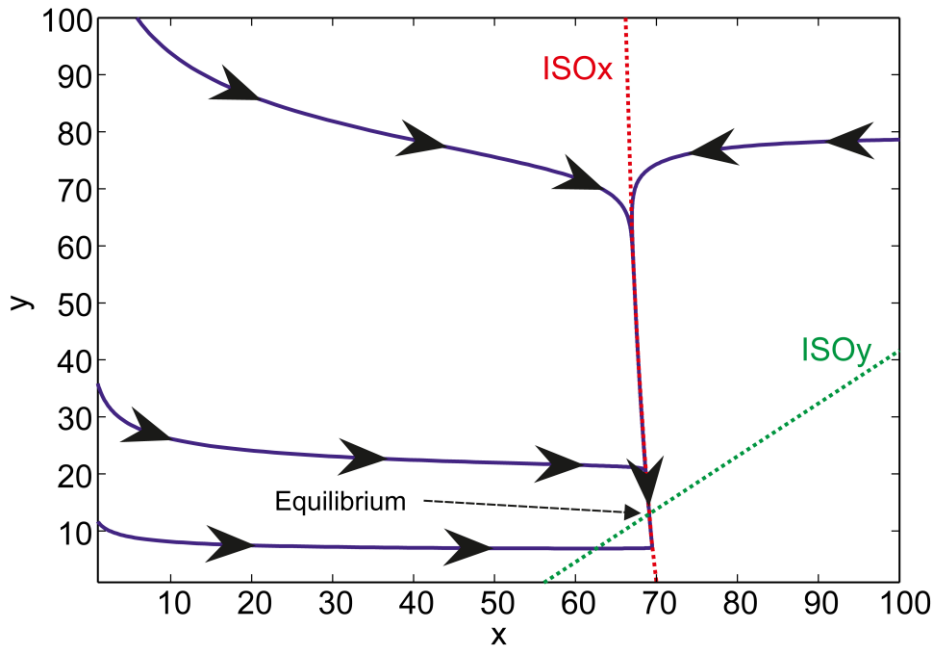
5 Figure 2. Isoclines and solutions for the three-individual encounter model with parameters of  
6 Numerical example 2. Stable coexistence at equilibrium  $(x^*, y^*) = (69.92, 10.25)$ . Programed in  
7 MatLab environment.

8

9 Figure 3. Stable coexistence as function of intrinsic growth rate of prey  $r_1$  and the energetic value  
10 of a prey  $c_4$ . Programed in MatLab environment.

11

1 Figure 1 COLOUR FOR WEB AND TO BE PRINTED IN BLACK-AND-WHITE



2

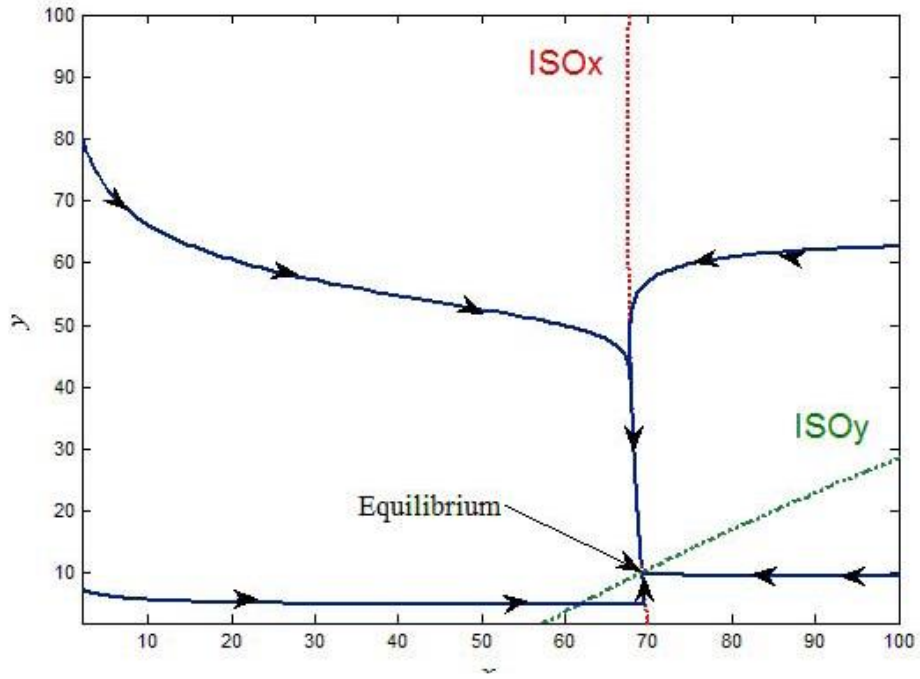


1 **Figure 2**

2 COLOUR FOR WEB AND TO BE PRINTED IN BLACK-AND-WHITE

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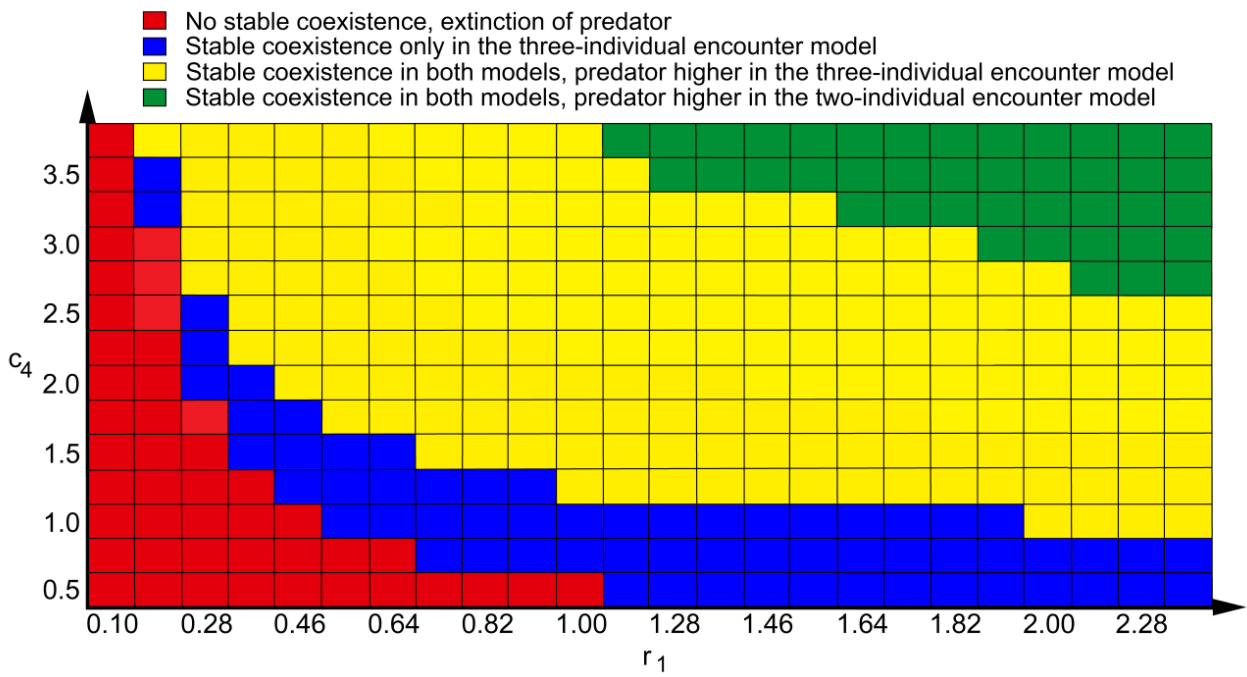
8

1 Figure 3

2 COLOUR FOR WEB

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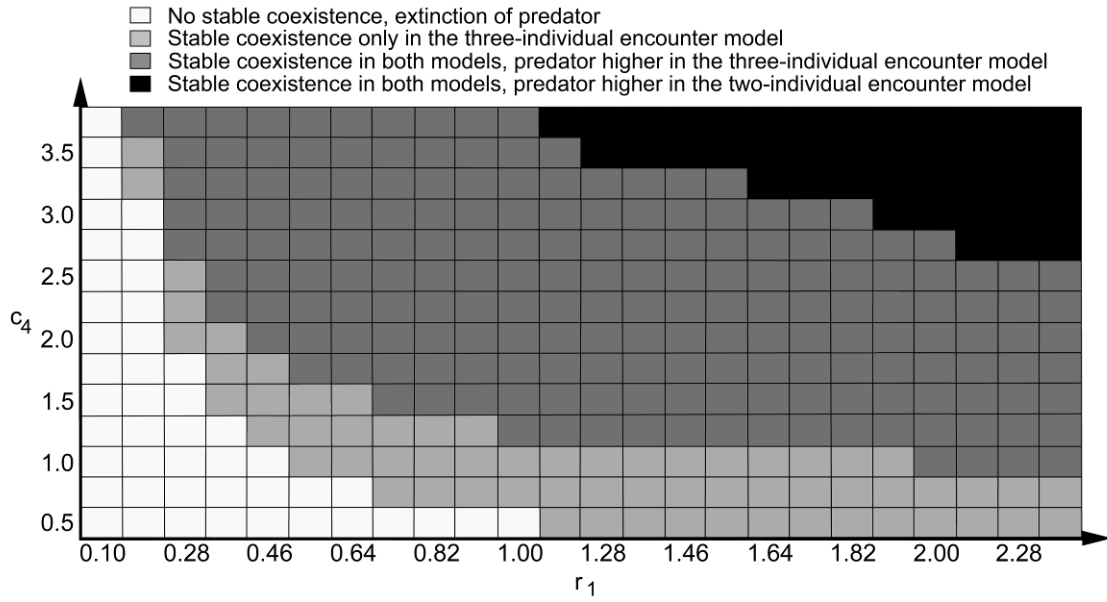
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1 Figure 3

2 TO BE PRINTED IN BLACK-AND-WHITE



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## Appendix 1. Coexistence

3

Below we deal with the consistence of the model and the coexistence of both species.

4

### A) When is dynamics (1) bounded?

5

The prey population is obviously bounded for  $x > \bar{x} := \frac{r_1}{a}$ , since  $\dot{x} < 0$ , for all  $y \geq 0$ , and for

6

$0 < x \leq \bar{x}$ , the growth of the prey is also limited. Thus the question arises: When is the predator

7

also bounded for  $x > 0$ ? For all  $x > 0$  we need a  $y_x > 0$ , such that for all  $y > y_x$  we have

8

$$-r_2 - \sum_{i=1}^3 \frac{c_i p_i(x, y)}{\sum_j T_j p_j(x, y)} + c_4 \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} < 0.$$

9

10 An easy calculation shows that with notation  $c_m := \min \{c_1, c_2, c_3\}$ , the latter inequality is equivalent

11 to

12

$$(c_4 + c_m)p_4(x, y) < c_m.$$

13 If for all fixed  $x > 0$ , we have  $\lim_{y \rightarrow \infty} p_4(x, y) = 0$ , then the latter inequality clearly holds, implying

14 the boundedness of dynamics (1). In biological terms, if for fixed prey density, the functional

15 response tends to zero, then dynamics (1) is bounded.

### 16 B) When do both species coexist in dynamics (1)?

1 Assume that dynamics (1) is bounded. Now the question arises: Is the set of points  $(x,0)$   
 2  $(0 \leq x \leq \bar{x})$  a repeller to the interior of the positive half-plane? This question splits into two sub-  
 3 questions:

4 **B.1. When does prey not die out?** Clearly, if  $r_2$  is greater than the intake by the functional  
 5 response for prey density near zero, then equilibrium  $(0, 0)$  is a saddle.

6  
 7 **B.2. When can predator survive?**

8 If  $y=0$ , then  $x(t)$  tends to  $\bar{x}$ , thus the question is whether  $\dot{y} > 0$  holds at  $(\bar{x}, y)$ , for all  
 9 sufficiently small  $y > 0$ . It is not hard to see that

10 
$$-r_2 - \sum_{i=1}^3 \frac{c_i p_i(x, y)}{\sum_j T_j p_j(x, y)} + c_4 \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} > 0$$

11 holds whenever

12 
$$(c_4 + c_M) \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} > r_2 + \frac{c_M}{\sum_j T_j p_j(x, y)},$$

13 where  $c_M := \max \{c_1, c_2, c_3\}$ . Since the activity probabilities continuously depend on the densities, it  
 14 is enough to suppose that

15 
$$(c_4 + c_M) \frac{p_4(\bar{x}, 0)}{\sum_j T_j p_j(\bar{x}, 0)} > r_2 + \frac{c_M}{\sum_j T_j p_j(\bar{x}, 0)}.$$

16 This inequality has the following implication: Consider a stable prey population without  
 17 predator, so the prey density is  $\bar{x}$ . If the predator arrives in this prey population, then there are  
 18 two possibilities: either the predator can establish a population when the above inequality holds,

1 or the predator cannot establish a population since the prey density is too small (in particular,  
 2 when the above inequality does not hold).

3

4 **C) Possible types of coexistence and existence of equilibrium**

5 In order to guarantee the coexistence in dynamics (1), we can apply the Poincaré-Bendixson  
 6 theorem (see e.g. Hofbauer & Sigmund 1988). Under the condition implying boundedness of  
 7 dynamics (1), the omega-limit set  $\omega$  corresponding to any initial value in the positive quadrant,  
 8 is not empty. Therefore, either a) there is an equilibrium in  $\omega$ , or b)  $\omega$  is a periodic orbit. Since  
 9 under the conditions of subsections B1 and B2, both  $(0,0)$  and  $(0,\bar{x})$  are saddles, an equilibrium  
 10 in  $\omega$  cannot be either of them. Therefore, in both cases a) and b) coexistence is obtained.  
 11 (Furthermore, a periodic orbit also surrounds an equilibrium.)

12

13 **Appendix 2. Local asymptotic stability by linearization**

14 For the brevity, let us rewrite system (1) with different notation:

15 
$$\dot{x} = x(r_1 - ax) - \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} y = F(x, y)$$

16 
$$\dot{y} = y \left( -r_2 + \frac{\sum_i \bar{c}_i p_i(x, y)}{\sum_j T_j p_j(x, y)} \right) = yG(x, y),$$

17 where constants  $\bar{c}_i := -c_i (i=1,2,3), \bar{c}_4 := c_4$  are introduced just for a more compact way of  
 18 writing. Assume that there exists an interior (i.e. positive) equilibrium  $(x^*, y^*)$ . Using the

1 linearization method, it is easy to see that for the local asymptotic stability of the equilibrium it is  
 2 sufficient that either the following Conditions (A.1) - (A.2) (3) and (A.3) - (A4) (5); or  
 3 Conditions (A.1) - (A.2) and (A.5) - (A.6) hold.

$$4 \quad \frac{\partial}{\partial x} F(x^*, y^*) < 0 \quad (A.1)$$

$$5 \quad \frac{\partial y^* G(x^*, y^*)}{\partial y} < 0 \quad (A.2)$$

$$6 \quad \frac{\partial}{\partial y} F(x^*, y^*) < 0 \quad (A.3)$$

$$7 \quad \frac{\partial y^* G(x^*, y^*)}{\partial x} > 0 \quad (A.4)$$

$$8 \quad \frac{\partial}{\partial y} F(x^*, y^*) > 0 \quad (A.5)$$

$$9 \quad \frac{\partial y^* G(x^*, y^*)}{\partial x} < 0 \quad (A.6)$$

10

11

12 **Conditions (A.1) - (A.2)**

13 Condition (A.1) implies that at the equilibrium the per capita growth rate of each population is a  
 14 partially decreasing function of its own abundance. With more details, for the prey

15  $\frac{\partial}{\partial x} F(x^*, y^*) < 0$  reads

$$16 \quad r_1 - 2ax^* < \frac{\partial}{\partial x} \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} y^* \quad (A.7)$$

1 Observe that  $r_1 - 2ax^*$  means the per capita prey growth rate without predation pressure, and

2  $\frac{\partial}{\partial x} \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} y^*$  is the marginal change in the consumption of the predator with respect to

3 the prey abundance. Thus (A.6) means that at the equilibrium, the growth rate of prey resulting  
 4 from the carrying capacity is less than the decay rate of prey abundance by the predation pressure  
 5 (i.e. less than the marginal rate of increase of the functional response with respect to the prey  
 6 abundance).

7 Condition (3) for the predator,  $\frac{\partial y^* G(x^*, y^*)}{\partial y} < 0$ , can be written as

$$8 \quad \frac{\partial}{\partial y} y \left( -r_2 + \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) = \left( -r_2 + \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) + y^* \left( \frac{\partial}{\partial y} \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) < 0.$$

9 Since  $(x^*, y^*)$  is an equilibrium, the latter inequality is equivalent to

$$10 \quad \frac{\partial}{\partial y} \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} < 0. \tag{A.8}$$

11 (A.8) implies that at the equilibrium the net energy intake from all activities is a strictly  
 12 decreasing function of the predator abundance.

13 Since at the equilibrium the net biomass intake of the predator is necessarily positive (i.e.

14  $\sum_i \bar{c}_i p_i(x^*, y^*) > 0$ ), we immediately obtain that (A.8) is equivalent to

$$15 \quad \frac{\frac{\partial}{\partial y} \sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_i \bar{c}_i p_i(x^*, y^*)} < \frac{\frac{\partial}{\partial y} \sum_j T_j p_j(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)}, \tag{A.9}$$



1 which means that at the equilibrium, the relative rate of increase of the net biomass intake with  
 2 respect to **the** prey abundance is smaller than the relative rate of increase of the average time  
 3 duration of an activity with respect to **the** predator abundance.

4

5 **Conditions (A.3) - (A4)**

6 Now let us consider Condition (A.3). For the prey population we get that  $\frac{\partial}{\partial y} F(x^*, y^*) < 0$  reads

7 as

8 
$$\frac{\partial}{\partial y} \left[ x^* (r_1 - ax^*) - \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} y^* \right] = - \frac{\partial}{\partial y} \left[ \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} y^* \right] < 0,$$

9 i.e.

10 
$$\frac{\partial}{\partial y} \left[ \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} y^* \right] > 0, \tag{A.10}$$

11 **which** implies that at the equilibrium the total killing (functional response multiplied by the  
 12 predator abundance) is a strictly increasing function of the abundance of the predator. Condition  
 13 (A.10) is equivalent to

14 
$$\frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} + y^* \frac{\partial}{\partial y} \frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} > 0.$$

15 Since  $\frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} > 0$ , (A.10) can be written as

1 
$$\frac{\frac{\partial p_4(x^*, y^*)}{\partial y \sum_j T_j p_j(x^*, y^*)}}{\frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)}} + \frac{1}{y^*} > 0,$$

2 or

3 
$$-\frac{\frac{\partial p_4(x^*, y^*)}{\partial y \sum_j T_j p_j(x^*, y^*)}}{\frac{p_4(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)}} < \frac{1}{y^*}. \tag{A.11}$$

4 Condition (A.11) means that, at the equilibrium, the relative rate of decrease of the functional  
 5 response with respect to the predator abundance, should be large enough. The smaller the  
 6 equilibrium predator abundance is, the higher this threshold is.

7 Now let us consider Condition (A4):  $\frac{\partial y^* G(x^*, y^*)}{\partial x} > 0$  is obviously equivalent to

8 
$$\frac{\partial}{\partial x} y \left( -r_2 + \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) = y \left( \frac{\partial}{\partial x} \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) > 0,$$

9 or

10 
$$\frac{\partial}{\partial x} \frac{\sum_i c_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} > 0. \tag{A.12}$$

11 (A.12) implies that at the equilibrium the net energy intake from all activities is a strictly  
 12 increasing function of the prey abundance. Furthermore, for (13) we get

$$\frac{\partial}{\partial x} \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} = \frac{\sum_j T_j p_j(x^*, y^*) \frac{\partial}{\partial x} \sum_i \bar{c}_i p_i(x^*, y^*) - \sum_i \bar{c}_i p_i(x^*, y^*) \frac{\partial}{\partial x} \sum_j T_j p_j(x^*, y^*)}{\left[ \sum_j T_j p_j(x^*, y^*) \right]^2} > 0,$$

2 or

$$\frac{\frac{\partial}{\partial x} \sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_i \bar{c}_i p_i(x^*, y^*)} > \frac{\frac{\partial}{\partial x} \sum_j T_j p_j(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)}. \quad (\text{A.13})$$

4 Condition (A.13) means that at the equilibrium the relative rate of increase of the net biomass  
 5 intake with respect to **the prey abundance is greater than the relative** rate of increase of the  
 6 average time duration of an activity with respect to **the predator abundance**.

7

8 **Remark** (An alternative form of Condition (A.4). Since at the equilibrium  $r_2 = \frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)}$ ,

9 and the time average is always positive,  $\frac{\partial y^* G(x^*, y^*)}{\partial x} > 0$  holds if and only if

$$\sum_i (\bar{c}_i - r_2 T_i) \frac{\partial}{\partial x} p_i(x^*, y^*) > 0. \quad (\text{A.14})$$

11 The  $i$ -th activity of **the** predator provides  $\bar{c}_i$  biomass intake during  $T_i$ . On the other hand,  **$r_2 T_i$**  is  
 12 the net biomass loss for the predator by doing nothing during  $T_i$ . Thus  $\sum_i (\bar{c}_i - r_2 T_i) p_i(x^*, y^*)$  is  
 13 the difference between the net biomass intake and the basic biomass loss for predator during the  
 14 average time of an arbitrary activity. (A.14) means that the marginal rate of this difference with  
 15 respect to **the** prey abundance is positive.

16 Condition (A5) - (A6) has a similar biological interpretation to that of Condition (A.3) - (A4).

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### Appendix 3. Global asymptotic stability by Lyapunov function

Now we give a general sufficient condition for global asymptotic stability of an interior equilibrium  $(x^*, y^*)$  of dynamics (1), with respect to the positive quadrant of the plane. We will say that  $(x^*, y^*)$  is *dissipative*, if for each positive abundance pair  $(x, y) \neq (x^*, y^*)$  we have

$$(x - x^*, y - y^*) \begin{pmatrix} \Phi(x, y) \\ \Psi(x, y) \end{pmatrix} < 0, \tag{A.15}$$

where  $\Phi(x, y)$  and  $\Psi(x, y)$  denote  $\frac{\dot{x}}{x}$  and  $\frac{\dot{y}}{y}$ , respectively. We use the term “dissipative” here based on the fact that the interaction decreases the biomass of the system, which is a generalization of the well-known notion of dissipativity in Lotka-Volterra systems. Now we show that inequality (A.15) implies global asymptotic stability of equilibrium  $(x^*, y^*)$  with respect to the positive quadrant.

It is easy to see that the Lyapunov function of the classical Lotka-Volterra model also works here. Indeed, for all positive pair  $(x, y) \neq (x^*, y^*)$  obviously

$$U(x, y) = x^* \left( \frac{x}{x^*} - \ln \frac{x}{x^*} - 1 \right) + y^* \left( \frac{y}{y^*} - \ln \frac{y}{y^*} - 1 \right) > 0,$$

and from  $gradU(x, y) = \left( \frac{x - x^*}{x}, \frac{y - y^*}{y} \right)$ , the derivative of  $U$  with respect to dynamics (1) is

$$DU(x, y) := (x - x^*)F(x, y) + (y - y^*)G(x, y) = (x - x^*, y - y^*) \begin{pmatrix} \Phi(x, y) \\ \Psi(x, y) \end{pmatrix} < 0.$$

Hence **the** global asymptotic stability of the equilibrium follows.

Finally we note that inequality (A.15) can be also written in the form

1

$$DU(x, y) = (x - x^*, y - y^*) \begin{pmatrix} \Phi(x, y) - \Phi(x^*, y^*) \\ \Psi(x, y) - \Psi(x^*, y^*) \end{pmatrix} < 0.$$

2