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



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HIGHLIGHTS

- Based on the activity distribution of the predator, we generalized Holling's basic idea for functional response.
- We derive a general dynamics from predator activities that makes it possible to study the influence of different activity distributions on the coexistence.
- The key finding highlights a difference when only predator–prey encounters are considered compared to predator–predator–prey encounters and indicates that the latter system can increase the predator abundance and the parameter space over which coexistence is stable.

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ABSTRACT

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

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

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1. Introduction

In biological systems the interactions between individuals take time. The functional response (see [Holling, 1959](#)) takes into account the handling time decreasing the number of active hunting predators. Furthermore, the abundance-dependent and time-consuming intra-specific interaction may decrease the

number of hunting predators. The idea that predator abundance has an effect on the functional response is well-studied in ecology ([Abrams, 1994](#); [Akçakaya et al., 1995](#); [Abrams and Ginzburg, 2000](#)). From a theoretical point of view, [Beddington \(1975\)](#) and [de Angelis et al. \(1975\)](#) independently introduced a functional response that accounts for the predators' interference.

From an experimental point of view, while [Fussman et al. \(2005\)](#) showed that the consumer has an effect on the functional response only at extraordinary high abundances, e.g. [Mech \(1977\)](#) found that the best fit functional response includes predator abundance dependence.

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

In this paper we will consider a one prey–one predator system: in the prey population there is an indirect competition (e.g. depletion of resources) and between the predators there is a direct interaction, i.e. when two predators encounter, they fight with each other. In this case the fight does not only take time, but we can also assume that during fighting the occasional injury may happen, and during recovery the predators stop all other activities, including hunting (Witz, 1990). Furthermore, fighting also decreases the biomass of the predators (Riechert, 1988). Our aim is to develop a model derivation method in which two ecological phenomena can be dealt with at the same time: intra-specific competition between predators (Chase et al., 2002), and time duration of predator activities. If the predator can do only one activity at a time, the interference between predators and the predation process is not independent, or putting it more explicitly: Holling (1959) emphasized the importance of time constraint in predation and Beddington (1975) and de Angelis et al. (1975) pointed out that the predators’ interference decreases the functional response. Now we are interested in the effect of the time constraint on the competition coefficient between predators, and on the functional response simultaneously, when predator competition and predation are not independent.

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

In Section 2 we introduce a general model for the considered situation. In Section 3, a particular class of the general model is studied: two-individual encounter models are considered where the focal individual cannot encounter with a prey and other predators at a time, in the same perception range. This is the consequence of the assumption that preys do not aggregate and are randomly distributed between perception ranges, and we can neglect the case when there is one prey and another predator in one perception range at the same time. The well-known Beddington–de Angelis model is obtained as a particular case of this class. In Section 4 the case is considered when the predator abundance is large enough, so the assumption that the focal predator does not encounter with a prey and a predator at the same time, is not acceptable. For simplicity, the independence of the prey and predator distributions is supposed. It is shown that these three-individual encounter models can lead to qualitatively different dynamic behaviour. In Section 5, simulation results of two- and three-individual encounter models are compared. Section 6 is dedicated to the discussion of the results. Finally, in Appendices A–C, conditions for the coexistence and asymptotic Lyapunov stability are obtained.

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

To derive the functional response we will consider the following class of the predation processes. Predator is only locally omniscient, which has two consequences: First, the predator can observe a prey and/or a conspecific only in a given “small” area called “perception range”. Second, before arriving, the predator has no information on a given perception range, thus it checks the perception ranges randomly.

The perception ranges are classified by their contents, they may be empty, contain a prey and/or a conspecific. The distribution of different perception ranges depends on the abundance of prey and predator. We will concentrate on a short time period T (for instance, one day), while the change in abundances can be neglected. In other words, during time T the predators cannot kill too many prey and/or other predators.

In summary, during the visiting process, the encounter probabilities depend on the prey and predator abundances; these encounter probabilities do not change during the time period T ; the focal predator finds a random series of different kind of perception ranges and all the following encounter events are independent.

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

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

In Table 1 below, T_i is the average time duration of the i -th activity, T_S is the searching time; T_F is the average “time cost” of fighting with a predator; T_M is the attack time and T_H is the digestion time. Let x be the abundance of prey and y that of the predator, $p_i(x, y)$ denotes the probability of i -th activity. E.g. $p_1(x, y)$ denotes the probability that the predator is searching in an empty perception range. We note that, these probabilities, apart from the abundances, may also depend on the spatial distribution of prey and predator (Kratina et al., 2007; Nachman, 2006); on habitat complexity (Hillebrand and Cardinale, 2004; Grabowski, 2004) and on the behaviour of predator and/or prey.

Finally, $0 < c_i$ denotes the net energy intake from the i -th activity: c_1 is the cost of searching,

c_2 is the average cost of fighting activity (cost of searching plus cost of fighting), c_3 is the cost of the activity of missed attack (cost of searching plus cost of attack), and c_4 is the value of activity of successful predation (the value of prey minus the cost of searching and cost of attack).

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

Now we derive the average number of predator–prey and predator–predator interactions, per unit time. These interaction

Table 1
General predator activity distribution.

Activity	Parameters		
	Duration time	Probability	Energy
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

rates depend on the abundances of the considered species and on the time duration of activities. We assume that during the considered time period T , the abundance of the prey and that of the predator does not change much. In other words, the activity distributions are constant functions of x and y within T . These assumptions allow us to use the same activity distributions during time period T , see Garay and Móri (2010). We have proved that in unit time, the expected number of i -th activities can be estimated by $(p_i(x, y) / \sum_j T_j p_j(x, y))$. The intuitive background of this estimation is the following: during time T , we take independent samples from the given activity distribution. Since the activity distribution does not change during T , the average time duration of an activity is $\sum_j T_j p_j(x, y)$. Thus during T , the average number of activity events is $(T / \sum_j T_j p_j(x, y))$. Based on independent repetitions, $p_i(x, y)$ part of the average number of activity events is the number of i -th activities. Thus during unit time, the expected number of i -th activities is estimated by $(p_i(x, y) / \sum_j T_j p_j(x, y))$. In particular, the functional response is given by $(p_4(x, y) / \sum_j T_j p_j(x, y))$, and the average number of fights during unit time is $(p_2(x, y) / \sum_j T_j p_j(x, y))$.

Now substituting the above interaction rates into the standard ecological model (e.g. Arditi et al., 2004), yields the following canonical population dynamics:

$$\begin{aligned} \dot{x} &= x(r_1 - ax) - \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} y \\ \dot{y} &= y \left(-r_2 - \sum_{i=1}^3 \frac{c_i p_i(x, y)}{\sum_j T_j p_j(x, y)} + c_4 \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} \right), \end{aligned} \quad (1)$$

where r_1 is the intrinsic growth rate of the prey, a/r_1 the carrying capacity for the prey, and r_2 is the intrinsic mortality rate of the predator. The novelty of dynamics (1) is that in each interaction rate it takes account of the time durations of all considered predator activities. For instance, the fight between predators is a kind of competition. In lots of dynamical models (see e.g. Haque, 2011, and the references therein) the competition coefficient does not depend on the time constraint in the predation process. However, if the predator can do only one activity at a time and each interaction has fixed average time duration, then the functional response and the competition coefficient are not independent, since the time constraints connect them, as we can see in dynamics (1).

2.1. Consistence of the model

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

2.2. Coexistence

Coexistence takes place if the prey can survive, and the predator can establish a population. Firstly, the prey does not die out, if r_2 is greater than the intake by the functional response when prey density is near zero. This condition seems natural, since it means that the predator cannot survive when the prey density is small enough. Secondly, as for the predator, coexistence is

guaranteed by the following minimal condition: consider a stable prey population without predator, then the prey density is r_1/a . If a predator arrives in this prey population, and the former can establish a population, then coexistence occurs (for details see Appendix A). Thirdly, if dynamics (1) is bounded and the two species coexist, then there is always an equilibrium or a periodic orbit of the dynamics (1). Fourthly, we note that since in dynamics (1), the probabilities of different activities are arbitrary continuous functions, all kinds of coexistence may happen: stable equilibrium or stable cycle (for details see Appendix A).

2.3. Stable equilibrium coexistence

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

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

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

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

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

In Appendix C we show that an appropriately defined dissipativity is a general sufficient condition for *globally stable coexistence in dynamics (1)* (i.e., for global asymptotic stability of an interior equilibrium). To this end, we adapted the notion of dissipativity of a Lotka–Volterra system to our case. The term “dissipative” here is 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 the Lotka–Volterra systems. We note that, in our case, in each interaction the biomass strictly decreases: the competition between prey and the interaction between predators has a negative effect on the biomass. Furthermore, during predation the biomass of the killed prey is greater than the increase in predator biomass, since there is a cost of attack and digestion as well. So, from a biological point of view, we think system (1) is usually dissipative, but we cannot prove this conjecture.

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

3. Two-individual encounter model

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

Suppose that the prey and predator distribution is well mixed in the home range of the predator, in a homogeneous field of H area units where the prey and predator abundances are x and y , respectively. Denote the area of a perception range of an individual predator by h , so in the considered field there are H/h perception ranges. Based on the above assumptions, x and y are the numbers of perception ranges where there is a solitary prey and a solitary predator, respectively. Furthermore, there are $H/h - x - y$ empty perception ranges. Since interactions occur only when an individual encounters another individual, first we have to calculate the probabilities of different encounter events.

In order to obtain encounter probabilities between zero and one, we have to assume that $H/h \gg x + y$. Now suppose that a focal predator individual encounters neither prey nor another predator with probability $d(0, 0) = 1 - (h/H)x - (h/H)y$, encounters a prey with probability $d(X, 0) = (h/H)x$, and encounters another predator with probability $d(0, Y) = (h/H)y$. For the sake of simplicity, here we assume that $y \approx y - 1$. A similar assumption is widely used in random processes.

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

Based on the above assumption we have the following activity distribution: No interaction happens with probability $p_1(x, y) = 1 - p_2(x, y) - p_3(x, y) - p_4(x, y)$, two predators fight with the probability $p_2(x, y) = (h/H)y$, a predator misses a prey with the probability $p_3(x, y) = (1 - k)(h/H)x$, and kills it with probability $p_4(x, y) = k(h/H)x$. Under the present assumptions we get the activity distribution given in Table 2.

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

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

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

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

Hence we get back the Beddington–de Angelis functional response, since the average number of prey killed per time unit is $(x/(H/h)T_S + T_F y + T_H x)$. We note that our functional response derivation method also gives back the classical Holling functional responses (see Garay and Móri 2010) as particular cases. The

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

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

Table 3
Predator activity distribution providing Beddington–de Angelis functional response.

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

dynamics (1) now reads

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

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

Here we strictly follow the steps of investigation of the general dynamics (1), but now we have a concrete activity distribution.

Firstly, each solution is bounded if for all $x \in]0, (r_1/a)[$, there exists y_x , such that for all $y > y_x$ we have $\dot{y} < 0$, which obviously holds with $\bar{y}_x = ((c_4 - r_2 T_H)/(c_2 + r_2 T_F))x - (r_2 T_S/(c_2 + r_2 T_F))(H/h)$. Therefore, the above dynamics is bounded.

Secondly, the predator can establish a population, if near equilibrium $((r_1/a), 0)$ of the above dynamics, $\dot{y} > 0$ holds, which is the case if

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

Thirdly, there exists an interior equilibrium

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

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

where $A = [T_F c_4 + T_H c_2]a$, $B = [((H/h)T_S a - r_1 T_H)c_2 + (1 - r_1 T_F)c_4 - r_2 T_H]$, $C = (H/h)T_S[r_1 c_2 + r_2]$.

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

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

Observe that the latter has the following sign structure

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

A well-known sufficient condition for the stability of the Jacobian matrix (i.e., for the negativity of the real part of each eigenvalue of J) is $\text{tr}J < 0$ and $\det J > 0$. The first inequality reads

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

Observe that a sufficient condition for the latter is

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

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

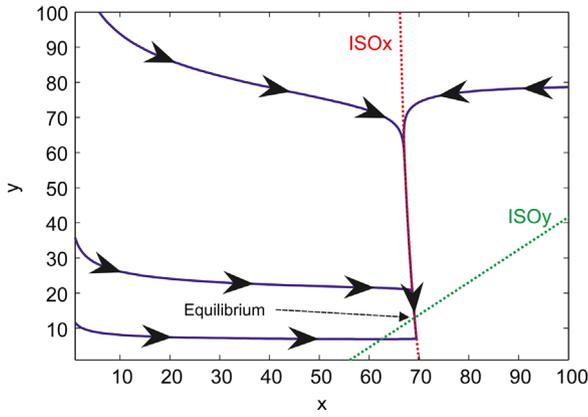


Fig. 1. Isoclines and solutions for the two-individual encounter model, with parameters of Numerical example 1. Stable coexistence at equilibrium $(x^*, y^*) = (69.07, 13.31)$. Programed in MatLab environment.

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

4. Three-individual encounter model

When the predator abundance is large enough, our previous assumption (that the focal predator does not encounter a prey and predator at the same time) is not reasonable (see Fussman et al., 2005). For the sake of simplicity, we assume that the prey and predator distributions are independent. Thus the focal predator individual encounters a prey only, with probability $d(X, 0) = (h/H)x(1 - (h/H)y)$, since the probability that one prey is in a given perception range is $(h/H)x$, the probability that another predator is in the same perception range, is $x(1 - (h/H)y)$. Furthermore, since the prey and the predator are independently distributed, $(h/H)x(1 - (h/H)y)$ is the probability that no prey and no another predator are in a perception range. Similarly, the focal predator encounters another predator only, with probability $d(0, Y) = (1 - (h/H)x)(h/H)y$, encounters another predator and a prey at a time with probability $d(X, Y) = (h/H)x(h/H)y$, and encounters neither prey nor another predator with probability $d(0, 0) = (1 - (h/H)x)(1 - (h/H)y)$. Moreover, assume when two predators meet, they always fight, thus the probability of a fight is $p_2(x, y) = d(0, Y) + d(X, Y) = (h/H)y$. Under these biological assumptions we get the activity distribution shown in Table 4.

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

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

$$\dot{y} = y\left(-r_2 + \frac{c_4k\frac{h}{H}x(1 - \frac{h}{H}y) - c_1(1 - \frac{h}{H})[x(1 - \frac{h}{H}y) + y] - c_2\frac{h}{H}y - c_3(1 - k)\frac{h}{H}x(1 - \frac{h}{H}y)}{T_S + T_F\frac{hy}{H} + T_M\frac{hx}{H} - T_M\frac{h^2xy}{H^2} + T_H\frac{khx}{H} - T_H\frac{kh^2xy}{H^2}}\right).$$

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

Numerical example 2. If we take the parameters of Numerical example 1, for the above dynamics we obtain that both the linearization method and the Lyapunov function method

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

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

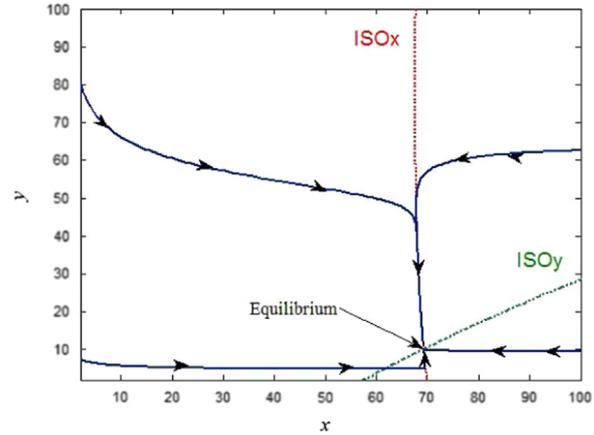


Fig. 2. Isoclines and solutions for the three-individual encounter model with parameters of Numerical example 2. Stable coexistence at equilibrium $(x^*, y^*) = (69.92, 10.25)$. Programed in MatLab environment.

(dissipativity) again imply stable coexistence at the interior equilibrium $(x^*, y^*) = (69.92, 10.25)$. The system turns out to be dissipative at this equilibrium, see Fig. 2.

5. Comparison of the above two models

The fight always decreases the equilibrium abundance of the predator, since the energy cost of fighting decreases the total predator biomass, and the time duration of fighting decreases the average number of hunting predators (in particular, during recovery the predator does not hunt). Consider both two-individual and three-individual encounter models at the same abundances. In the latter we assume that two predators always fight when they encounter, no matter whether there is a prey or not.

Based on this assumption, the probability of a fight is the same in both models. Furthermore, successful hunting has lower probability in the three-individual encounter model than in the two-individual one. In summary: in the three-individual encounter model there is a relatively higher fighting rate and a lower killing rate. Consequently, the functional response is smaller. This means that in the three-individual encounter model the same number of predators has a smaller effect on the prey abundance than in the two-individual one.

Thus, at first glance, one may expect the equilibrium predator abundance to be lower in the three-individual encounter model, since the prey surely survives in a three-individual encounter (because whenever two predators meet, they always fight). Simulations, however, show this is the case only when the conversion rate c_4 is high enough (see Fig. 3), and what is more, for fixed r_1 with growing c_4 , coexistence appears first in the three-individual encounter model, and then predator abundance is higher in this model than in the two-individual encounter model, when c_4 is still not too large, see Fig. 3.

A possible explanation to this is the following: let us consider a pair of parameters r_1 and c_4 where there is still no coexistence in

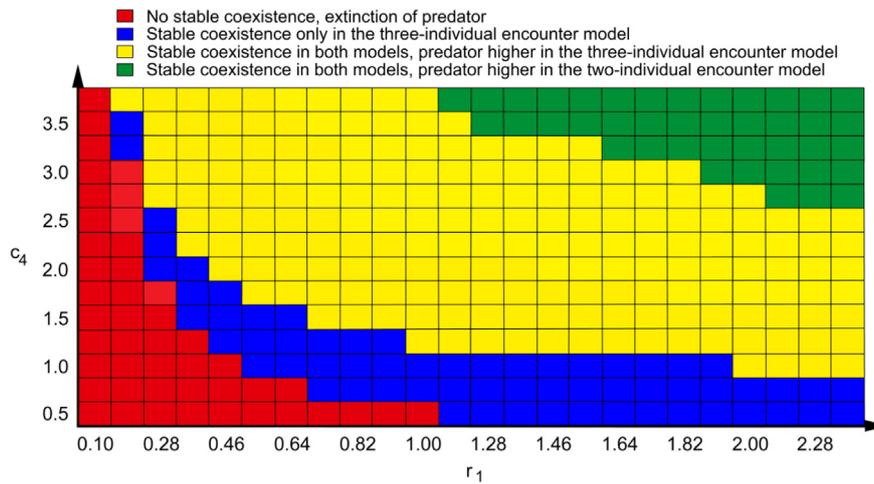


Fig. 3. Stable coexistence as a function of intrinsic growth rate of prey r_1 and the energetic value of a prey c_4 . Programmed in MatLab environment.

either of the two models. This means that the stably existing prey is not able to maintain the predator population. Now, for greater c_4 coexistence appears first in the three-individual encounter model, where the predator is less efficient, since its functional response is lower. The latter also results in more surviving prey per unit time, therefore the higher biomass production of the prey (per unit time) may maintain the predator population. Furthermore, in this parameter range, the equilibrium predator abundance is low, having only a slight effect on killing probability.

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

6. Discussion

6.1. Derivation of functional responses

Over the past decades, numerous functional responses have already been introduced (see Jeschke et al., 2002), since there is no single functional response that would well fit to any data set (Skalski and Gilliam, 2001). The main obstacle is that the functional response is very sensitive to the details of the biological situation considered. Under the assumption that during time T the abundances of interacting species do not change radically, our mechanism based method makes it possible to take into account the fine details of the biological case considered. Our method is very near the classical derivation of functional response by renewal theory (see McNamara and Houston, 1999), when under the assumption that the prey population immediately renews, the functional response is also the ratio of the encounter rate and the time average. We note that the encounter distribution and the activity distribution are not the same in general, since when a predator faces an encounter situation, it may use different strategies, e.g. when the predator encounters another predator then one of them may flee. In this strategic situation we obtain an ecological game (see Cressman et al., 2014). In present paper we have not considered ecological games.

6.2. Concerning the resulting functional responses

We considered the case when the predators not only hunt but also fight with each other. This is a particular case of predator

interference. Based on the activity distribution we also derived the Beddington–de Angelis functional response. We note that Geritz and Gyllenberg (2012), for example, using differential equation at quasi-steady state, also derived a Beddington–de Angelis type functional response, based on biological assumptions quite different from ours. While Geritz and Gyllenberg (2012) considered non-interacting predator and non-refuging prey, we considered a fight between predators and non-refuging prey. Thus, our resulting functional responses give a slight generalization of the original functional responses of Beddington (1975) and de Angelis et al. (1975), shedding a new light on them.

6.3. About stable coexistence

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

Our observation that coexistence appears first in the three-individual encounter model may have an important implication for modelling methodology. In modelling, three-individual encounters (interactions) are usually neglected based on the following reasons: *first*, two-individual interactions are more probable. *Second*, higher-order encounters usually increase the non-linearity of the model, thus its analysis becomes harder. However, we have found that when the equilibrium abundance of the predator is small (thus the three-individual encounters are very improbable), coexistence appears first in the three-individual encounter model.

Now the question arises whether the number of encounters between predators is high enough to modify the functional response. We mention two possibilities: *first*, the territorial behaviour (and the dispersal of young predators) decreases the interaction between predators, but does not rule it out. The scanning of the territory and fighting with intruder conspecifics take time (including recovery time), thus the time for predation attacks should be decreased by predator interference, and hence the latter can increase the survival of prey. For instance, it was observed that wolves hunted little at the borders of their territory in order to avoid fatal encounters with neighbours, thus in the buffer zone of wolf packs' territories the survival rate of deer is higher (Mech, 1977). Furthermore, territorial behaviour

decreases the local predator abundance. Based on our observation that predator interference ensures coexistence with not so fecund and not so valuable prey, we think a territorial predator establishes a population more easily than a non-territorial one, when their prey is not so fecund and not so valuable. *Second*, cleptoparasitism is also a predator interference that needs energy and time (Broom and Rychtar, 2013), for which a three-individual encounter is necessary. The cleptoparasitism increases the survival rate of prey, when decreasing the functional response, if the time duration of cleptoparasitization is greater than the searching time (thus the denominator of the functional response, i.e. the time average of one activity increases) and the encounter probability of two predators is positive (thus the numerator of the functional response, i.e., the probability to encounter only one prey, decreases). Although, a predator must have killed a prey before cleptoparasitization occurs, in this case the prey surely does not survive under predator interference. Furthermore, during cleptoparasitization, the predator is either injured or falls victim of a cannibal attack (Nilsson and Bronmark, 1999), which also increases the predation pressure on the prey.

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

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Appendix A. Coexistence

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

(a) When is dynamics (1) bounded?

The prey population is obviously bounded for $x > \bar{x} := (r_1/a)$, since $\dot{x} < 0$, for all $y \geq 0$, and for $0 < x \leq \bar{x}$, the growth of the prey is also limited. Thus the question arises: When is the predator also bounded for $x > 0$? For all $x > 0$ we need a $y_x > 0$, such that for all $y > y_x$ we have

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

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

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

If for all fixed $x > 0$, we have $\lim_{y \rightarrow \infty} p_4(x, y) = 0$, then the latter inequality clearly holds, implying the boundedness of dynamics (1). In biological terms, if for fixed prey density, the functional response tends to be zero, then dynamics (1) is bounded.

(b) When do both species coexist in dynamics (1)?

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

(b.1.) When does the prey not die out?

Clearly, if r_2 is greater than the intake by the functional response for prey density near zero, then equilibrium $(0, 0)$ is a saddle.

(b.2.) When can the predator survive?

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 sufficiently small $y > 0$. It is not hard to see that

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

holds whenever

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

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

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

This inequality has the following implication: Consider a stable prey population without predator, so the prey density is \bar{x} . If the predator arrives in this prey population, then there are two possibilities: either the predator can establish a population when the above inequality holds, or the predator cannot establish a population since the prey density is too small (in particular, when the above inequality does not hold).

(c) Possible types of coexistence and existence of equilibrium

In order to guarantee the coexistence in dynamics (1), we can apply the Poincaré–Bendixson theorem (see e.g. Hofbauer and Sigmund, 1988). Under the condition implying boundedness of dynamics (1), the omega-limit set ω corresponding to any initial value in the positive quadrant, is not empty. Therefore, either (a) there is an equilibrium in ω , or (b) ω is a periodic orbit. Since under the conditions of subsections b.1 and b.2, both $(0, 0)$ and $(0, \bar{x})$ are saddles, an equilibrium in ω cannot be either of them. Therefore, in both cases of (a) and (b) coexistence is obtained. (Furthermore, a periodic orbit also surrounds an equilibrium.)

Appendix B. Local asymptotic stability by linearization

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

$$\begin{aligned} \dot{x} &= x(r_1 - ax) - \frac{p_4(x, y)}{\sum_j T_j p_j(x, y)} y = F(x, y) \\ \dot{y} &= y \left(-r_2 + \frac{\sum_i \bar{c}_i p_i(x, y)}{\sum_j T_j p_j(x, y)} \right) = yG(x, y), \end{aligned}$$

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 writing. Assume that there exists an interior (i.e. positive) equilibrium (x^*, y^*) . Using the linearization method, it is easy to see that for the local asymptotic stability of the equilibrium it is sufficient that either the following Conditions (A.1) and (A.2) (3) and (A.3) and (A.4) (5); or Conditions (A.1) and (A.2) and (A.5) and (A.6) hold.

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

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

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

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

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

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

Conditions (A.1) and (A.2)

Condition (A.1) implies that at the equilibrium the per capita growth rate of each population is a partially decreasing function of its own abundance. With more details, for the prey $(\partial/\partial x) F(x^*, y^*) < 0$ reads

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

Observe that $r_1 - 2ax^*$ means the per capita prey growth rate without predation pressure, and $(\partial/\partial x)(p_4(x^*, y^*)/\sum_j T_j p_j(x^*, y^*))y^*$ is the marginal change in the consumption of the predator with respect to the prey abundance. Thus (A.6) means that at the equilibrium, the growth rate of prey resulting from the carrying capacity is less than the decay rate of prey abundance by the predation pressure (i.e. less than the marginal rate of increase of the functional response with respect to the prey abundance).

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

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

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

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

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

Since at the equilibrium the net biomass intake of the predator is necessarily positive (i.e. $\sum_i \bar{c}_i p_i(x^*, y^*) > 0$), we immediately obtain that (A.8) is equivalent to

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

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

Conditions (A.3) and (A.4)

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

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

i.e.

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

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

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

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

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

or

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

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

Now let us consider Condition (A.4): $(\partial y^* G(x^*, y^*)/\partial x) > 0$ is obviously equivalent to

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

or

$$(\partial/\partial x) \left(\frac{\sum_i \bar{c}_i p_i(x^*, y^*)}{\sum_j T_j p_j(x^*, y^*)} \right) > 0. \tag{A.12}$$

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

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

or

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

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

Remark. (An alternative form of Condition (A.4). Since at the equilibrium $r_2 = (\sum_i \bar{c}_i p_i(x^*, y^*)/\sum_j T_j p_j(x^*, y^*))$, and the time average is always positive, $(\partial y^* G(x^*, y^*)/\partial x) > 0$ holds if and only if

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

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 the net biomass loss for the

predator by doing nothing during T_i . Thus $\sum (\bar{C}_i - r_2 T_i) p_i(x^*, y^*)$ is the difference between the net biomass intake and the basic biomass loss for predator during the average time of an arbitrary activity. (A.14) means that the marginal rate of this difference with respect to the prey abundance is positive.

Conditions (A.5) and (A.6) have a biological interpretation similar to that of Conditions (A.3) and (A.4).

Appendix C. Global asymptotic stability by the 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

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

where $\Phi(x, y)$ and $\Psi(x, y)$ denote (\dot{x}/x) and (\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 the 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 pairs $(x, y) \neq (x^*, y^*)$ 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 $\text{grad}U(x, y) = \left((x - x^*/x), (y - y^*/y) \right)$, the derivative of U with respect to dynamics (1) is

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

Hence the global asymptotic stability of the equilibrium follows.

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

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

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