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## Mathematical Models for Host-Parasitoid Interactions


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# Contents

# Preface

The present diploma thesis provides insight into the mathematical modeling of the interaction between a parasitoid population and its host species. It offers an introduction and analysis of some models (including possible generalizations) as well as mathematical background in the theory of difference equations. Additionally, the biological interpretation of the systems treated is taken into account.

My motivation for this thesis was to present the application of mathematical theory to processes in nature. I chose the topic of host-parasitoid interactions since it was only at the beginning of the 20th century that the mathematical treatment of this field started and today its meaning to ecology is still growing continuously. Mathematical modeling of biological pest control and integrated pest management (IPM) is especially needed in agriculture, where parasitoids have proved themselves to be particularly effective in the fight against insect pests. Recent publications of Gu (2009), Singh (2009), Sun (2009) and Tang (2008), for example, treating pest control and IPM, respectively, show the importance of some profound knowledge of mathematics in biological fields.

## Acknowledgments

At this point I want to thank my supervisor O. Univ.-Prof. Dr. Karl Sigmund, who supported me during the writing of this thesis. I would also like to express my thanks to Ryusuke Kon, PhD, for his helpful comments and suggestions as well as his useful emendations. Furthermore, I am very much obliged to my parents Jaqueline and Johannes Lajtos, who always encouraged me during my formation and made it possible for me to complete my course of education. And last but not least, I want to thank Raimund Mathias Porod for his helpful explanations and discussions during my study of mathematics.

# 1 Introduction and Overview

## 1.1 Introduction

### 1.1.1 Biological Background and Terms

This diploma thesis provides an insight into different models and dynamics of host-parasitoid interactions. Most host-parasitoid relationships can be found in insects. Indeed, 10% or more of metazoan species are parasitoids.[1]
The models that will be introduced were developed during the last century. The ecological meaning of parasitoid species for pest control is growing continuously because parasitoids have proved themselves to be capable of suppressing the abundance of insect pests. Hence, the importance of a profound understanding of host-parasitoid interactions is still increasing.[2]
Before any analysis of the host-parasitoid models can be done, some biological terms will be introduced:[3]

**Parasitoid/Host:** A parasitoid is an organism that spends a significant portion of its lifetime in or on a single organism. In order to fulfill its life cycle it eventually has to kill this organism. The organism that harbors the parasitoid is called host.

Parasitoids can be classified[4]

- by the host stage they attack:
  There are egg parasitoids, larval parasitoids and pupal parasitoids. Parasitoid species that attack adult hosts are very rare.
  Parasitoids with arrested development attack an early host stage but emerge from and kill another stage. These are called egg-larval parasitoids, larval-pupal parasitoids etc., depending on the host stage attacked and killed.

- by the way they lay their eggs:
  Ectoparasitoids just lay their eggs on the outside of the host's body

[1] Schreiber 2007, p. 273
[2] Schreiber 2007, p. 273
[3] van Driesche & Bellows jr. 1996, p. 23
[4] Hassell 2000, p. 2; van Driesche & Bellows jr. 1996, pp. 37 f.

and the parasitoids' larvae then develop externally. Endoparasitoids, on the other hand, inject their eggs right into their host's body where the larvae then feed and develop.

- by their effects on the host's physiology:
  Koinobionts attack their host but do not kill them at once. The parasitoids benefit from the continued life and feeding of their host. Idiobionts prevent their host from further developing, e. g. by paralyzing it, after the host was attacked.

- by the number of parasitoids that can develop to maturity on or in a single host:
  Parasitoid species where only one parasitoid per host is able to develop are referred to as solitary parasitoids. Parasitoids are called gregarious if one host is able to support the development of more than one parasitoid.

- by their egg-limitation:[5]
  Synovigenic parasitoids continuously produce eggs over their lifetime. They experience egg-limitation if the number of hosts they encounter in a day is greater than the daily amount of eggs they are able to produce. Pro-ovigenic parasitoids are equipped with a fixed number of eggs they are born with. If the number of hosts they encounter during their lifetime exceeds this fixed number of eggs, they cannot lay any more eggs.

- by their ability to use other parasitoids as hosts:
  In contrast to primary parasitoids, secondary parasitoids or hyperparasitoids eventually attack other parasitoid species.
  If an already parasitized host is again attacked by a parasitoid by the same species, one speaks of superparasitism. If this second parasitic attack is performed by a parasitoid of another species, this is referred to as multiparasitism.

[5]Schreiber 2007, p. 274

### 1.1.2 Host-Parasitoid Interaction Models

This section introduces and analyzes two simple 2-species models for one host and one parasitoid population. The populations are assumed to exhibit discrete, synchronized generations. This model structure provokes a one-generation time lag between the parasitic act and the resulting change in the host population's density. Hence, the treated systems consist of 2 recurrence equations that yield on the one hand, the density of the hosts' eggs in generation $t+1$ and on the other hand, the density of the adult female parasitoids in generation $t+1$.[6] The density of the susceptible host stage is assumed to be equal to the density of the hosts' eggs. This means that all host eggs are able to develop to the susceptible host stage, i. e. the population density is not influenced by predation, competition etc.

$$\begin{aligned} H_{t+1} &= \lambda H_t g(H_t, P_t) f(H_t) \\ P_{t+1} &= \omega H_t (1 - g(H_t, P_t)) \end{aligned} \tag{1}$$

or

$$\begin{aligned} H_{t+1} &= \lambda H_t g(P_t) f(H_t) \\ P_{t+1} &= \omega H_t (1 - g(P_t)) \end{aligned} \tag{2}$$

The function $g(H_t, P_t)$ or $g(P_t)$ represents the fraction of hosts escaping from parasitism in each generation.[7] It can depend either both on $H_t$ and $P_t$ as it is found in the original Thompson model[8] and its generalizations (1) or just on $P_t$ as it is the case for the original Nicholson-Bailey model[9] and its generalizations (2).[10] The terms $1 - g(H_t, P_t)$ and $1 - g(P_t)$ describe the

[6] Hassell 2000, p. 9

[7] Getz & Mills, pp. 335 f.

[8] Thompson 1924, pp. 69-89

[9] Nicholson & Bailey 1935, pp. 551-598

[10] In this diploma thesis, the Thompson model and the Nicholson-Bailey model will always be referred to as the original Thompson model and the original Nicholson-Bailey model.

fraction of hosts being parasitized. The form of the escape function $g$ varies depending on the distribution of parasitism events. Either the parasitoids are assumed to be randomly distributed among the hosts, which means that the escape function $g$ is realized as the zero term of the Poisson distribution:[11]

$$g(E) = \exp(-E) \tag{3}$$

Or, if $g$ is meant to model non-random or aggregated attacks of the parasitoid species, the escape function obeys the negative binomial distribution:[12]

$$g(E) = \left(1 + \frac{E}{k}\right)^{-k} \tag{4}$$

where $E$ is given by[13]

$$E = \frac{aP_t}{H_t}$$

in case of the Thompson model or by

$$E = bP_t$$

for the Nicholson-Bailey model.
Further, $k > 0$ is the so-called negative binomial aggregation parameter.[14] For $g$, expression (3) can be considered as the limiting case of (4) with $k = \infty$.[15] More detailed analysis, derivation and information about the forms of the escape function $g$ will be given in section 7.
The factor $f(H_t)$ stands for the fraction of hosts surviving density-dependent mortality, for example caused by intra-specific competition. Here $f$ is just dependent on $H_t$ what means that although parasitism precedes density-dependence, the fraction of hosts dying due to density-dependent factors is determined by the initial host density prior to parasitism. Indeed, this assumption can be found in nature:[16] Just consider the larvae of the winter moth (Operophtera brumata) at Wytham Wood and their parasitoid fly

[11] Elaydi 1999, p. 211
[12] Schreiber 2006, pp. 720 f.
[13] Getz & Mills 1996, p. 335
[14] Getz & Mills 1996, p. 337
[15] Schreiber 2006, p. 721
[16] May et al. 1981, p. 856

(Cyzenis albicans). The parasitoid attacks the host in its larval stage. Afterwards, the host species suffers from density-dependent mortality in its pupal stage, dependent on the density of healthy and parasitized hosts, i. e. on $H_t$. Since this death due to density-dependence affects the parasitized hosts as well, there are models where the factor $f(H_t)$ appears both in the recurrence equation for the host species and in the equation describing the parasitoid species' density. Hence, equation $P_{t+1}$ would be

$$P_{t+1} = \omega \times \underbrace{(1 - g(H_t, P_t))f(H_t)}_{\text{density of paras. hosts that survive dens. depend.}}$$

or

$$P_{t+1} = \omega \times \underbrace{(1 - g(P_t))f(H_t)}_{\text{density of paras. hosts that survive dens. depend.}}$$

respectively. These models are even more appropriate for the situation described.[17] The density-dependent survival function $f$ could also depend on $H_t g(H_t, P_t)$ or on $H_t g(P_t)$, respectively. In this case, parasitism and death due to these parasitic attacks act prior to density-dependent mortality and $f$ is therefore only dependent on the density of hosts having escaped from parasitism.[18] In some models, like in the original Thompson or the original Nicholson-Bailey model, the density-dependent survival function $f$ is assumed to fulfill $f(H_t) \equiv 1$. So there is no factor that regulates the growth of the host species in absence of parasitism. These models suggest that the host density grows exponentially when there is no interference of parasitoids. The parameter $\lambda$ represents the average number of eggs laid per host, $\omega$ is the average number of adult female parasitoids that emerge from one parasitized host. Both parameters are assumed to be constant, they could also be density-dependent.[19]

The following graphic shows a typical development of the host and the parasitoid species' density, respectively. It was derived from a generalized

[17] May et al. 1981, pp. 856-858
[18] May et al. 1981, pp. 858 f.
[19] Hassell 2000, pp. 10 f.

Nicholson-Bailey model given by

$$\begin{aligned} H_{t+1} &= \lambda H_t \left(1 + \tfrac{bP_t}{k}\right)^{-k} \tfrac{1}{1+cH_t^d} \\ P_{t+1} &= \omega H_t \left(1 - \left(1 + \tfrac{bP_t}{k}\right)^{-k}\right) \tfrac{1}{1+cH_t^d} \end{aligned}$$

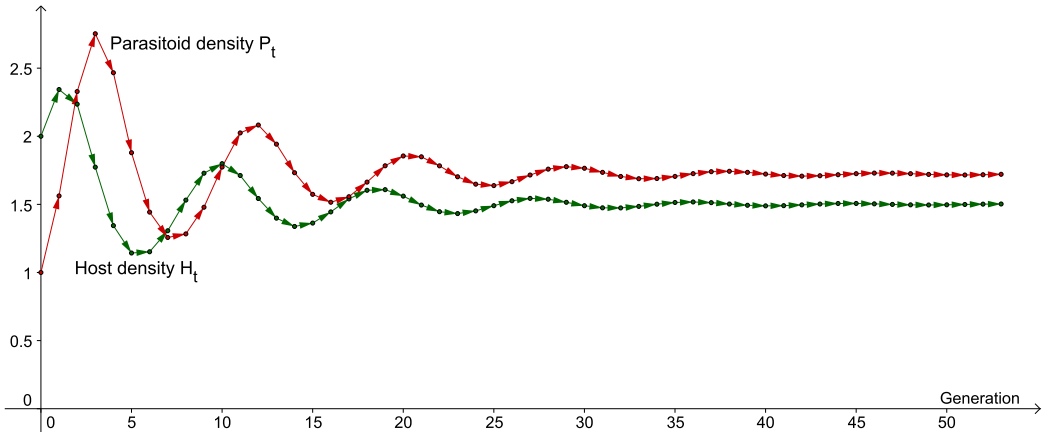



Fig. 1: The parameters are given by $a = 0.5$, $c = 0.5$, $d = 0.5$, $k = 1$, $\lambda = 3$, $\omega = 4$. The initial conditions are $H_0 = 2$ and $P_0 = 1$. From generation $t = 46$ on, the host density $H_t$ stays at a value of 1.5 while the parasitoid density $P_t$ stays at 1.72 from generation $t = 49$ on. The densities of both species reach a state of equilibrium at $(1.5, 1.72)$.

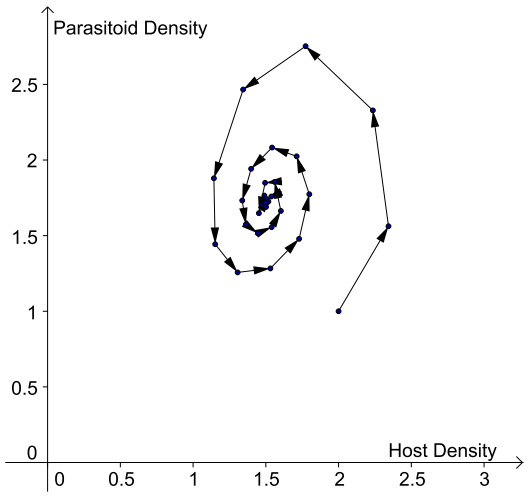



Fig. 2: This figure shows the corresponding phase diagram. The dynamics are converging to the fixed point $(1.5, 1.72)$.

## 1.2 Overview

Section 2 will provide useful definitions and mathematical means to determine the existence and stability of fixed points of discrete dynamical systems.

In section 3 the original Thompson model and its derivation are introduced followed by the analysis of a special generalization of the Thompson model[20]. The work of Schreiber will provide the five different dynamics of this system. Biological interpretation is given as well.

Section 4 is devoted to a more detailed analysis and computation of the original Thompson model and the Thompson model with aggregated search. The investigations will show that both systems do not have inner fixed points.[21]

Section 5 introduces the Nicholson-Bailey model and one special generalization, the Beddington model. The work of Kon will reveal its dynamics.[22]

[20]Schreiber 2006, pp. 719-725

[21]Only in case of one special condition there exist infinitely many fixed points in both systems.

[22]Kon 2006, p. 172-183

Section 6 presents the dynamics of the original Nicholson-Bailey model. The investigations will reveal that the inner equilibrium of the original Nicholson-Bailey model is stabilized if the parasitic attacks are assumed to be aggregated.

Section 7 treats the derivation and analysis of the escape function $g$ for both the generalized Thompson and generalized Nicholson-Bailey model. It will be shown that the assumption for the distribution of the parasitoids determines the form of $g$.

Section 8 concludes the thesis with the analysis of the density-dependent survival function $f$.

# 2 Mathematical Concepts

This section provides some mathematical prerequisites that will be useful for mathematical analysis in the upcoming sections.
We will first give the definition of a dynamical system.[23]

**Definition 2.1.**
*A dynamical system on the metric space* $(X, d)$ *is a mapping* $\pi\colon X \times G \to X$, *where* $G$ *is some set, satisfying*

1. $\pi(x, 0) = x \ \forall x \in X$ *(identity axiom)*
2. $\pi(\pi(x, t_1), t_2) = \pi(x, t_1 + t_2) \ \forall x \in X$ *and* $\forall \ t_1, \ t_2 \in G$ *(group axiom)*
3. $\pi$ *is continuous (continuity axiom)*

Throughout this thesis, the metric space $X$ is assumed to be $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n : x_i \geq 0 \, \forall i\}$ with the Euclidean metric $d(x, y) = \sqrt{(x_1 - y_1)^2 + \cdots + (x_n - y_n)^2}$.
We will investigate 1- or 2-dimensional discrete semi-dynamical systems. Therefore, set $G$ is replaced by $\mathbb{Z}_+$.
For example, $x' = f(x) = \pi(x, 1)$ generates a discrete dynamical system if all solutions are defined and $f$ is continuous.[24] If function $f$ is given by the Ricker map $f(x) = \lambda x \exp(-cx)$, we obtain a discrete semi-dynamical system.

From now on, we will use

$$x_{n+1} = f(x_n) \tag{5}$$

to denote a discrete dynamical system.[25] Above all, the existence and stability properties of fixed points of dynamical systems will be of interest.

[23] LaSalle 1976, p. 2
[24] LaSalle 1976, p. 2
[25] Elaydi 1999, p. 1

**Definition 2.2.**[26]
*A point $x^*$ in the domain of $f$ is said to be an equilibrium point (fixed point, rest point) of (5) if it is a fixed point of $f$, i. e. $f(x^*) = x^*$.*

**Definition 2.3.**[27]
*Let $x^*$ be a fixed point of (5).*
*$x^*$ is stable* $:\Leftrightarrow$ $\forall\varepsilon > 0\ \exists\delta > 0$ *such that* $\mid x_0 - x^* \mid < \delta \Rightarrow \mid f^n(x_0) - x^* \mid < \varepsilon\ \forall n \geq 0$
*$x^*$ is attracting* $:\Leftrightarrow$ $\exists\delta > 0$ *such that* $\mid x_0 - x^* \mid < \delta \Rightarrow \lim_{n\to\infty} x_n = x^*$
*$x^*$ is asymptotically stable* $:\Leftrightarrow$ *$x^*$ is stable and attracting*
*$x^*$ is unstable* $:\Leftrightarrow$ *$x^*$ is not stable*

**Definition 2.4.**[28]
*A point $p$ is a $k$-periodic point* $:\Leftrightarrow$ $f^k(p) = p$ *and* $f^j(p) \neq p$ *for* $j = 1, \ldots, k-1$.
*The set $\{p, f(p), \ldots, f^{k-1}(p)\}$ is a periodic orbit of period $k$ or a $k$-cycle.*

A well-known result to determine the local stability of a fixed point of a 1-dimensional dynamical system is provided by the following theorem:

**Theorem 2.1.**[29]
*Let $x^*$ be a fixed point of the difference equation (5) with $f\colon I \subset \mathbb{R} \to \mathbb{R}$ and $f$ is continuously differentiable at $x^*$. The following statements then hold true:*

1. $|\frac{d}{dx} f(x^*)| < 1 \Rightarrow$ *$x^*$ is asymptotically stable*
2. $|\frac{d}{dx} f(x^*)| > 1 \Rightarrow$ *$x^*$ is unstable*

In order to obtain similar results for systems of arbitrary dimension we have to introduce the following definitions:

[26] Elaydi 1999, p. 8
[27] Elaydi 1999, pp. 10 f.
[28] Elaydi 1999, p. 29
[29] Elaydi 1999, p. 22

**Definition 2.5.**[30]
*The spectral radius of a $n \times n$ -matrix $A$ is defined as $\rho(A) := \max_{1 \leq i \leq n} |\lambda_i|$, where $\lambda_i$ is an eigenvalue of $A$.*

**Definition 2.6.**[31]
*Let $x^*$ be a fixed point of the difference equation (5) with*

$$f = \begin{pmatrix} f_1 \\ \vdots \\ f_n \end{pmatrix}$$

*continuously differentiable at $x^*$. The Jacobian matrix of $f$ at $x^*$ is defined as*

$$Df(x^*) := \begin{pmatrix} \frac{\delta f_1}{\delta x_1}(x^*) & \cdots & \frac{\delta f_1}{\delta x_n}(x^*) \\ \vdots & \ddots & \vdots \\ \frac{\delta f_n}{\delta x_1}(x^*) & \cdots & \frac{\delta f_n}{\delta x_n}(x^*) \end{pmatrix}.$$

**Definition 2.7.**[32]
*A fixed point $x^*$ of (5) is called hyperbolic if all eigenvalues $\lambda_i$ of $Df(x^*)$ fulfill $|\lambda_i| \neq 1$, $i = 1, \ldots n$.*

**Theorem 2.2.**[33]
*Let $x^*$ be a hyperbolic fixed point of (5) with $f \in C^1$.*

1. *$\rho(Df(x^*)) < 1 \Rightarrow x^*$ is asymptotically stable*

2. *$\rho(Df(x^*)) > 1 \Rightarrow x^*$ is unstable*

[30] Elaydi 1999, p. 142
[31] Hofbauer & Sigmund 1992, p. 54
[32] Plaschko & Brod 1995, p. 10
[33] Elaydi 1999, p. 169

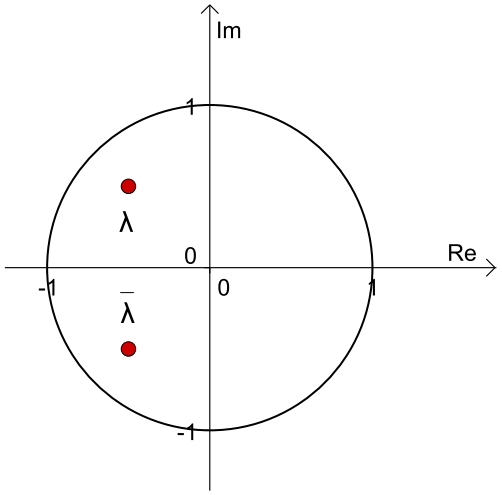



Fig. 3: The complex eigenvalue $\lambda$ and its complex conjugate $\bar{\lambda}$ lie within the unit circle.

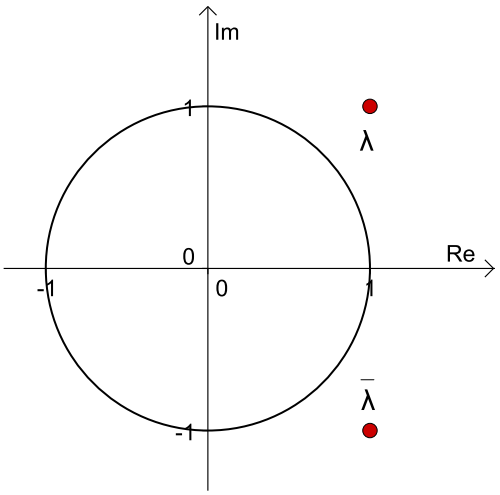



Fig. 4: The complex eigenvalue $\lambda$ and its complex conjugate $\bar{\lambda}$ lie out of the unit circle.

For 2-dimensional systems a special case of the so-called Jury criterion provides at the same time a necessary and sufficient condition for the eigenvalues of the corresponding Jacobi-matrix to fall within the unit circle.[34]

[34]Caswell 2001, p. 522

**Theorem 2.3.**
*Let $A$ be a $2 \times 2$-matrix.*
*If and only if the three conditions*

$$\begin{aligned} 1 - \operatorname{tr}(A) + \det(A) &> 0 \\ 1 + \operatorname{tr}(A) + \det(A) &> 0 \\ 1 - \det(A) &> 0 \end{aligned}$$

*are fulfilled, the spectral radius $\rho(A)$ is less than 1.*
*The Jury criterion can be pooled in the following inequality:*

$$\rho(A) < 1 \Leftrightarrow 2 > 1 + \det(A) > |\operatorname{tr}(A)|$$

*Proof:*[35]
The characteristic polynomial $p$ of a $2 \times 2$-matrix $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ is given by

$$\begin{aligned} p(\lambda) &= \det(A - \lambda I) \\ &= (a - \lambda)(d - \lambda) - cb \\ &= \lambda^2 + ad - \lambda(a + d) - bc \\ &= \lambda^2 - \lambda \operatorname{tr}(A) + \det(A) \end{aligned}$$

Since one obtains the eigenvalues by setting $p(\lambda)$ equal to 0, the eigenvalues $\lambda_{1/2}$ are given by

$$\lambda_{1/2} = \frac{\operatorname{tr}(A) \pm \sqrt{\operatorname{tr}^2(A) - 4 \det(A)}}{2}.$$

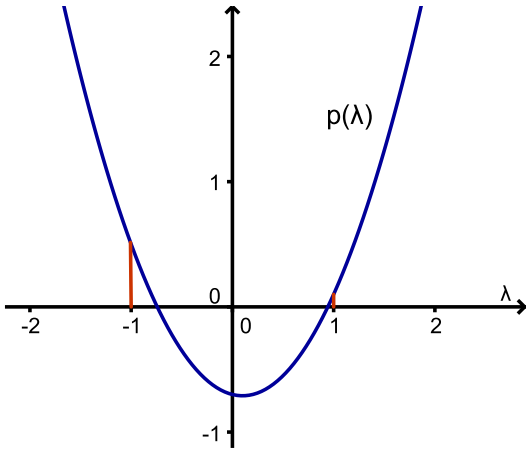
($\Rightarrow$)

First, suppose that we are treating real eigenvalues. In this case, the discriminant

$$\operatorname{tr}^2(A) - 4 \det(A)$$

[35] Elaydi 2008, pp. 200-203

is greater or equal to 0.
Since $\rho(A)$ is less than one, both eigenvalues $\lambda_1$ and $\lambda_2$ lie between $-1$ and 1. Furthermore, it is easy to see that $p(\lambda)$ is a convex function.




Hence, $p(-1)$ and $p(1)$ are greater than 0. This observation implies that

$$p(\pm 1) = 1 \mp \mathrm{tr}(A) + \det(A) > 0.$$

Since $|\lambda_i|$, $i = 1, 2$, is less than 1, the product of the two eigenvalues is less than 1 as well. This implies that $\det(A) = \lambda_1 \lambda_2 < 1$.

Secondly, assume the two eigenvalues $\lambda_1$ and $\lambda_2$ to be complex conjugates $\lambda$ and $\bar{\lambda}$. In this case, the discriminant

$$\mathrm{tr}^2(A) - 4\det(A)$$

is less than 0.
Since $\rho(A)$ is less than one, the absolute value of $\lambda$ is less than 1. Consequently, the product of the two eigenvalues and hence, the determinant of $A$ is less than 1 as well. We rewrite

$$\mathrm{tr}^2(A) - 4\det(A) < 0$$

as

$$\left(\frac{\mathrm{tr}(A)}{2}\right)^2 < \det(A). \tag{6}$$

Inequality (6) leads to

$$1 \pm \mathrm{tr}(A) + \det(A) > 1 \pm \mathrm{tr}(A) + \left(\frac{\mathrm{tr}(A)}{2}\right)^2. \tag{7}$$

The right hand-side of (7) can be written as $\left(1 \pm \frac{\mathrm{tr}(A)}{2}\right)^2$, which is obviously greater or equal to 0. As a consequence, the left hand-side of (7) is strictly greater than 0.

One implication of the proof is done.

($\Leftarrow$)

Assume we are treating the case

$$\mathrm{tr}^2(A) - 4\det(A) \geq 0.$$

Then

$$\begin{array}{rcl} \mid \lambda_{1/2} \mid & = & \frac{1}{2} \mid \mathrm{tr}(A) \pm \sqrt{\mathrm{tr}^2(A) - 4\det(A)} \mid \\ & < & \frac{1}{2} \mid \mathrm{tr}(A) \pm \sqrt{(\det(A)+1)^2 - 4\det(A)} \mid \\ & < & \frac{1}{2}\left(\det(A) + 1 + \sqrt{(\det(A)-1)^2}\right) \\ & = & \frac{1}{2}\left(\det(A) + 1 - (\det(A) - 1)\right) \\ & = & 1 \end{array} .$$

Now for

$$\mathrm{tr}^2(A) - 4\det(A) < 0$$

the calculations yield

$$\begin{array}{rcl} \mid \lambda_{1/2} \mid & = & \frac{1}{2} \mid \mathrm{tr}(A) \pm i\sqrt{-\mathrm{tr}^2(A) + 4\det(A)} \mid \\ & = & \frac{1}{2}\sqrt{\mathrm{tr}^2(A) + 4\det(A) - \mathrm{tr}^2(A)} \\ & = & \sqrt{\det(A)} \\ & < & 1. \end{array}$$

In case of complex eigenvalues $\lambda$, $\bar{\lambda}$ the inequality

$$\det(A) < 1$$

implies that

$$\lambda\bar{\lambda} = \det(A) < 1.$$

Since

$$| \lambda |^2 = \lambda\bar{\lambda} = | \bar{\lambda} |^2$$

we obtain $\lambda < 1$ and $\bar{\lambda} < 1$. In particular, the spectral radius $\rho(A)$ is less than 1.

□

# 3 The Thompson Model

## 3.1 Introduction

The original Thompson model

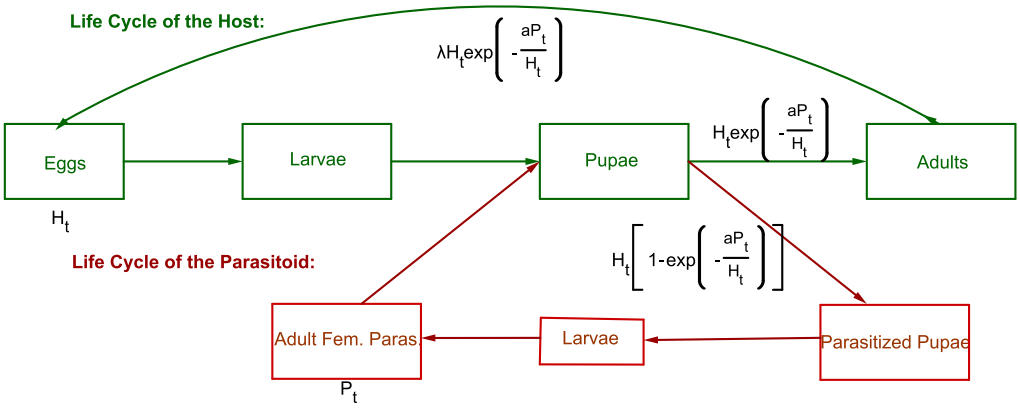
$$\begin{aligned} H_{t+1} &= \lambda H_t g(E) \\ P_{t+1} &= H_t(1 - g(E)) \end{aligned} \tag{8}$$

with $g(E) = \exp(-E)$ was developed by William Robin Thompson[36] in 1924. It was the first model describing host-parasitoid interactions. It contains an escape function $g$ that has the form of an exponential function. Further on, $\omega$ is assumed to be equal to 1, hence, this model treats the case of solitary parasitoids.[37] The system exhibits egg-limitation for the parasitoid. Egg-limitation means that the parasitoids are limited in the number of eggs they can produce or lay on hosts.[38] Therefore, the mean number of parasitoid eggs laid per host $E$ is given by

$$E = \frac{aP_t}{H_t} \tag{9}$$

where $a$ is the mean number of eggs laid by each female parasitoid among the host population.[39]
The following graphic illustrates the original Thompson model (8).

[36] Thompson 1924, pp. 69-89
[37] cf. solitary parasitoids in 1.1.1
[38] cf. synovigenic/pro-ovigenic parasitoids in 1.1.1
[39] Getz & Mills 1996, pp. 335 f.; Schreiber 2006, pp. 719 f.




While the original Thompson model neglects density-dependent factors influencing the host population's growth, its generalization[40]

$$H_{t+1} = \lambda H_t g\left(\frac{P_t}{H_t}\right) f(H_t) \tag{10}$$

$$P_{t+1} = \omega H_t \left(1 - g\left(\frac{P_t}{H_t}\right)\right) f(H_t) \tag{11}$$

with $g(x) = \left(1 + \frac{ax}{k}\right)^{-k}$ or $g(x) = \exp(-ax)$, includes a density-dependent survival function denoted by $f$ in addition to the escape function $g$. This special model suggests that the host experiences parasitism prior to density-dependent mortality. Furthermore, hosts do not die at once after being parasitized but continue to develop for some time. Therefore, parasitized hosts are involved too in density-dependent mortality due to intraspecific competition, emigration, predation etc. This assumption leads to the factor $f(H_t)$ in the equation for the parasitoid population density in generation $t + 1$.[41] The fact that density-dependent mortality precedes mortality arising from parasitism explains why $f$ is dependent on the entire host density of the $t$-th generation $H_t$.[42].

Furthermore, by defining $H_{t+1} = 0 = P_{t+1}$ whenever $H_t = 0$, the generalized Thompson model (10), (11) is continuously extended,[43] as can be easily seen:

[40] Schreiber 2006, p. 720

[41] This phenomenon is also described in 1.1.2.

[42] Kon & Schreiber 2009, p. 961; May et al. 1981, pp. 856-859; Schreiber 2006, p. 720

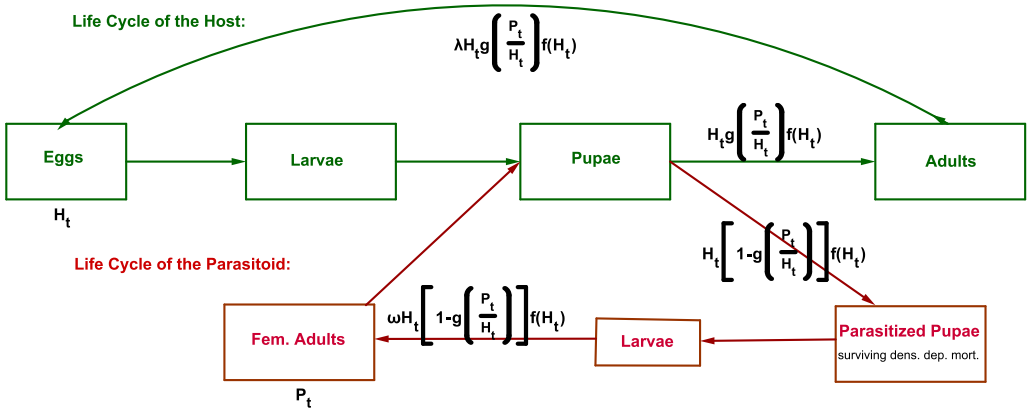
[43] Schreiber 2006, p. 721

$$H_{t+1} = \lambda \underbrace{H_t}_{\to 0} \underbrace{g\left(\frac{P_t}{H_t}\right)}_{\leq 1} \underbrace{f(H_t)}_{\leq 1} \to 0$$

$$P_{t+1} = \omega \underbrace{H_t}_{\to 0} \underbrace{\left(1 - g\left(\frac{P_t}{H_t}\right)\right)}_{\leq 1} \underbrace{f(H_t)}_{\leq 1} \to 0$$

for $H_t \to 0$ and arbitrary $k > 0$.

The graphic below illustrates the generalized Thompson model (10), (11):



## 3.2 Dynamics of the Generalized Thompson Model

This section is devoted to the analysis of the generalized Thompson model (10), (11). First, the following assumptions are made:[44]

- T0 The parameters $\lambda$, $\omega$, $a$ fulfill $\lambda$, $\omega$, $a > 0$.

- T1 $f$ is a continuous, non-increasing, positive function such that $f(0) = 1$ and $\lim_{x\to\infty} xf(x)$ exists (possibly infinite).

- T2 $g(x) = (1 + \frac{ax}{k})^{-k}$ with $k \in (0, \infty]$ where $k = \infty$ corresponds to $g(x) = \exp(-ax)$.

These assumptions cover the case where $f(H) \equiv 1$, so the following results are also true for the original Thompson model. Other possible choices of the survival function $f$ can be the generalized Beverton-Holt function[45] $f(H) = \frac{1}{1+cH^d}$ with $c \geq 0$, $d > 0$, the Ricker function[46] $f(H) = \exp(-cH)$ with $c \geq 0$, or the Hassell function[47] $f(H) = \frac{1}{(1+cH)^d}$ with $c \geq 0$, $d \geq 0$ . The survivorship function $f$ will be studied in more detail in section 8.
An observation of $g$ shows that it is a decreasing function,

$$\frac{dg(x)}{dx} = (-k)\left(1 + \frac{ax}{k}\right)^{-(k+1)} \frac{a}{k} < 0$$

or

$$\frac{dg(x)}{dx} = (-a)\exp(-ax) < 0,$$

respectively, for all $x \geq 0$, with $g(0) = 1$ and $\lim_{x\to\infty} g(x) = 0$. So, $0 < g(x) \leq 1$ for all $x \geq 0$.

[44] Schreiber 2006, p. 721; Kon 2009, p. 961
[45] Berezansky & Braverman 2004, pp. 851-868
[46] Ricker 1954, pp. 559-623; Schreiber 2003, pp. 201-209
[47] Hassell 1975, pp. 283-295

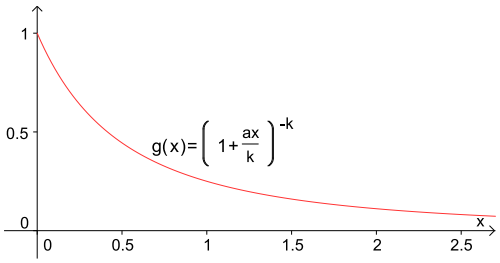



Fig. 5: Function $g$ is given by $(1 + \frac{ax}{k})^{-k}$ with $a = 2$ and $k = 2$.

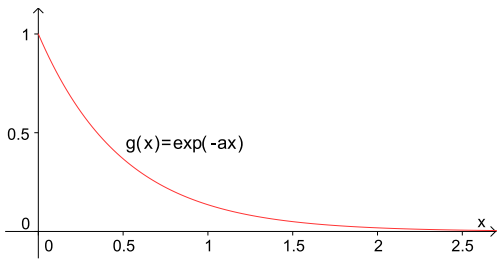



Fig. 6: Function $g$ is given by $\exp(-ax)$ with $a = 2$.

**Theorem 3.2.1.**[48]
*The generalized Thompson model (10), (11) satisfying T0-T2 exhibits five types of dynamics:*

1. *Host failure:*
   *If* $\lambda < 1$, *then*
   $$\lim_{t\to\infty}(H_t, P_t) = (0,0)$$
   *for any initial condition* $H_0 > 0$ *and* $P_0 \geq 0$.

2. *a) Parasitoid driven extinction and b) Coexistence:*
   *If* $\lambda > 1$ *and* $\omega a > \lambda$, *then there exists* $k^* \in (0,1)$ *and* $M > 0$ *such that*
   $$\lim_{t\to\infty}(H_t, P_t) = (0,0)$$
   *whenever* $k > k^*, H_0 > 0$ *and* $P_0 > 0$, *and*
   $$\liminf_{t\to\infty} H_t \geq M \qquad \liminf_{t\to\infty} P_t \geq M$$
   *whenever* $k < k^*$, $H_0 > 0$ *and* $P_0 > 0$. *Moreover, for* $k \in (0, k^*)$ *there exists* $y^*$ *(depending on* $k$*) such that*
   $$\lim_{t\to\infty} \frac{P_t}{H_t} = y^*$$
   *whenever* $H_0 > 0$ *and* $P_0 > 0$.

3. *Unconditional parasitoid failure:*
   *If* $\lambda > 1$, $\lambda > \omega a$ *and* $k \leq 1$, *then there exists* $M > 0$ *such that*
   $$\liminf_{t\to\infty} H_t \geq M \qquad \lim_{t\to\infty} \frac{P_t}{H_t} = 0$$
   *for any initial condition* $H_0 > 0$ *and* $P_0 > 0$.

4. *Conditional parasitoid failure:*
   *If* $\lambda > 1$, $\lambda > \omega a$ *and* $k > 1$, *then there exists* $y^* > 0$ *and* $M > 0$ *such that*
   $$\lim_{t\to\infty}(H_t, P_t) = (0,0)$$

[48] Schreiber 2007, pp. 276 f.; Schreiber 2006, pp. 721 f.

*whenever* $P_0 > y^* H_0 > 0$, *and*

$$\liminf_{t\to\infty} H_t \geq M \qquad \lim_{t\to\infty} \frac{P_t}{H_t} = 0$$

*whenever* $0 \leq P_0 < y^* H_0$. *Moreover,* $y^*$ *is a decreasing function of* $k > 1$.

Before the proof of this important theorem is shown, the biological meaning of this theorem is illustrated.[49]
The upcoming figures represent the dynamics of

$$\begin{aligned} H_{t+1} &= \lambda H_t (1 + \tfrac{aP_t}{kH_t})^{-k} \tfrac{1}{1+cH_t^d} \\ P_{t+1} &= \omega H_t (1 - (1 + \tfrac{aP_t}{kH_t})^{-k}) \tfrac{1}{1+cH_t^d} \end{aligned} \tag{12}$$

where the generalized Beverton-Holt function $f(H) = \frac{1}{1+cH^d}$ is used as density-dependent survival function.

ad 1. The case $\lambda < 1$ implies host failure because the reproductive rate is insufficient for the host species to sustain itself. The offspring produced is just not enough for the species to survive.[50]
A possible phase-diagram for $H_t$ and $P_t$ with $\lambda < 1$ is

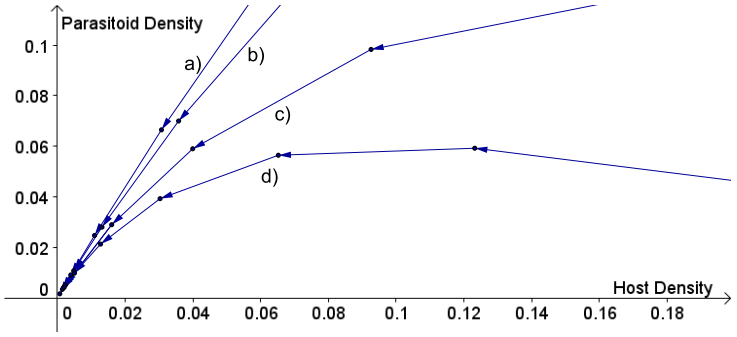



Fig. 7: The parameters are $\lambda = 0.86$, $\omega = 1.4$, $a = 1.7$, $c = 0.5$, $d = 1$, $k = 0.86$. Cases a)-d) were yield by using different initial conditions a) $H_0 = 100$, $P_0 = 101$; b) $H_0 = 4$, $P_0 = 2$; c) $H_0 = 100$, $P_0 = 2$; d) $H_0 = 600$, $P_0 = 1$

[49]Schreiber 2006, p. 722
[50]Schreiber 2006, p. 722

ad 2.a) Parasitoid driven extinction means that the host species will be extinct no matter what the initial conditions for the host and the parasitoid might look like.[51]

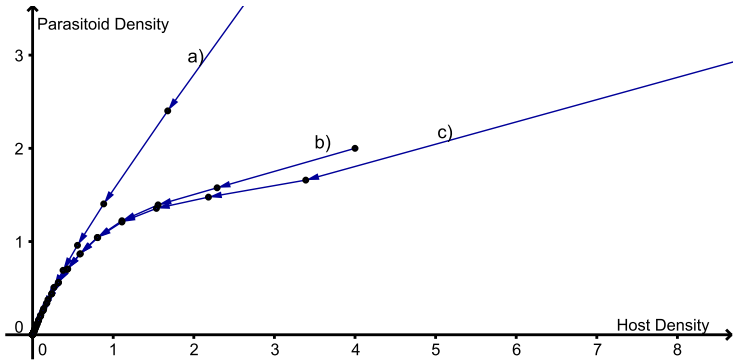



Fig. 8: The parameters are given by $a = 3.8$, $c = 0.5$, $d = 1$, $k = 0.66$, $\lambda = 4.2$, $\omega = 2$; a) $H_0 = 8$, $P_0 = 10$; b) $H_0 = 4$, $P_0 = 2$; c) $H_0 = 9$, $P_0 = 3$

ad 2.b) In this case, namely coexistence, both the host and the parasitoid species are able to persist independently of the given positive initial conditions. Besides, the long-term behaviour of this two-species system is given by[52]

$$\begin{aligned} H_{t+1} &= \lambda H_t f(H_t) g(y^*) \\ P_t &= y^* H_t \end{aligned}$$

where $y^*$ is the positive solution to $y = \frac{\omega}{\lambda}\left(\frac{1}{g(y)} - 1\right)$.[53]

[51] Schreiber 2006, p. 722
[52] Schreiber 2006, p. 722
[53] This expression will be explained on page 27.

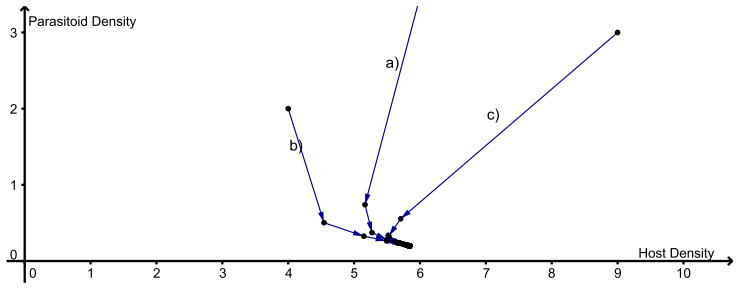



Fig. 9: The parameters are given by $a = 3.8$, $c = 0.5$, $d = 1$, $k = 0.06$, $\lambda = 4.2$, $\omega = 2$; a) $H_0 = 8$, $P_0 = 10$; b) $H_0 = 4$, $P_0 = 2$; c) $H_0 = 9$, $P_0 = 3$

ad 3. Unconditional parasitoid failure occurs when the ratio of the introduced parasitoid species and the host species converges to zero while the host population persists for any positive initial condition. Self-limitation of the host population implies that the parasitoids go extinct.[54]

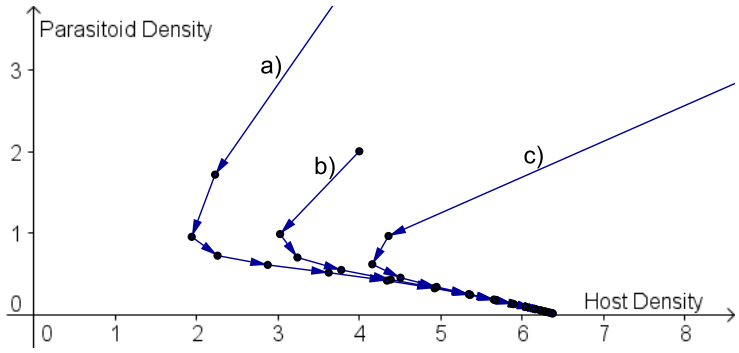



Fig. 10: The parameters are given by $a = 1.8$, $c = 0.5$, $d = 1$, $k = 0.86$, $\lambda = 4.2$, $\omega = 1.6$; a) $H_0 = 8$, $P_0 = 10$; b) $H_0 = 4$, $P_0 = 2$; c) $H_0 = 9$, $P_0 = 3$

ad 4. In the case of conditional parasitoid extinction the persistence of the host population strongly depends on the initial conditions. Either both species go to extinction or, if the parasitoid-host ratio is not sufficiently high, the host population will survive while the parasitoids die out.[55]

[54]Schreiber 2006, p. 722
[55]Schreiber 2006, p. 722

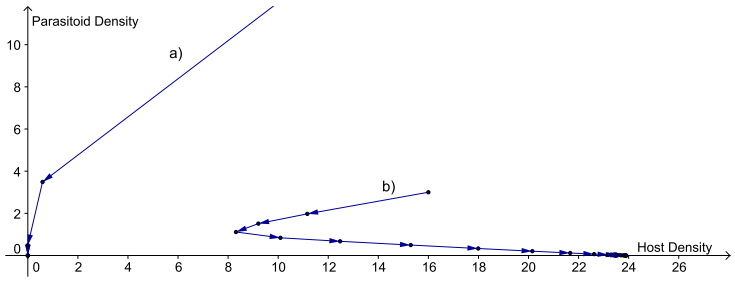



Fig. 11: The parameters are given by $a = 2.8$, $c = 0.9$, $d = 0.5$, $k = 28$, $\lambda = 5.4$, $\omega = 1.4$; a) $H_0 = 10$, $P_0 = 12$; b) $H_0 = 16$, $P_0 = 3$;

In order to provide a better understanding of the diverse dynamics of the generalized Thompson model under the conditions given in Theorem 3.2.1. case 2., we will take a closer look at system (12) under the conditions mentioned.

The following graphics show the development of the host and the parasitoid species' density, respectively, depending on the parameter $k$. The results illustrated below are obtained by the analysis of system (12).

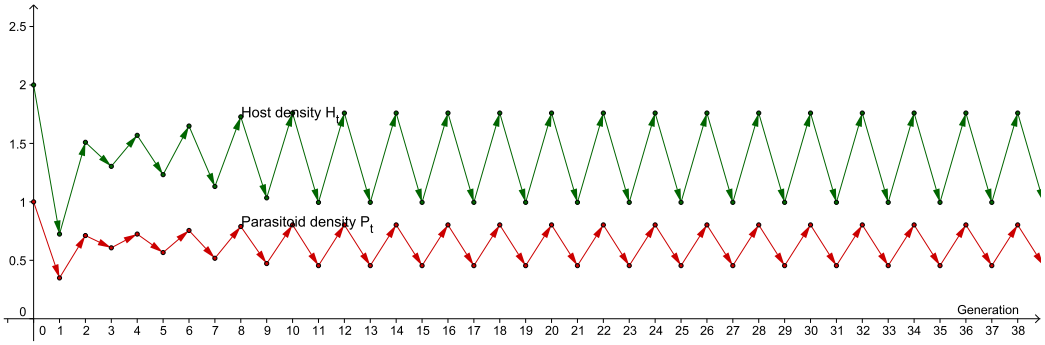



Fig. 12: The parameters are given by $a = 4.7$, $c = 0.3$, $d = 4.1$, $k = 0.35$, $\lambda = 4.55$, $\omega = 2.1$. The initial conditions are $H_0 = 2$ and $P_0 = 1$. The host density $H_t$ varies alternately from 1 to 1.76 from generation $t = 11$ on. The parasitoid density $P_t$ changes from 0.8 to 0.45 from generation $t = 12$ onwards.

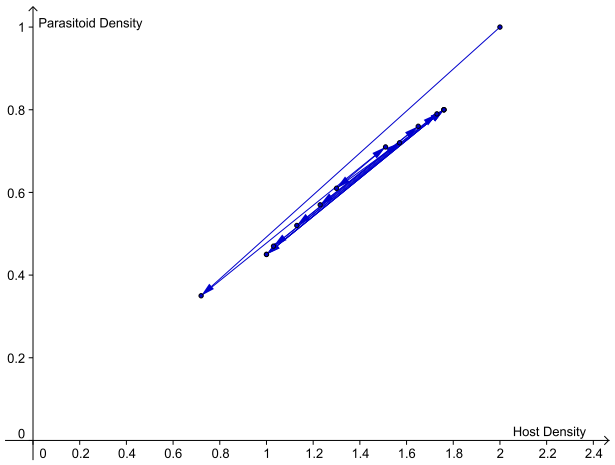



Fig. 13: This figure shows the corresponding phase diagram.

The dynamics of the system above are periodic. However, if on slightly modifies the value of $k$, the system even has a fixed point:[56]

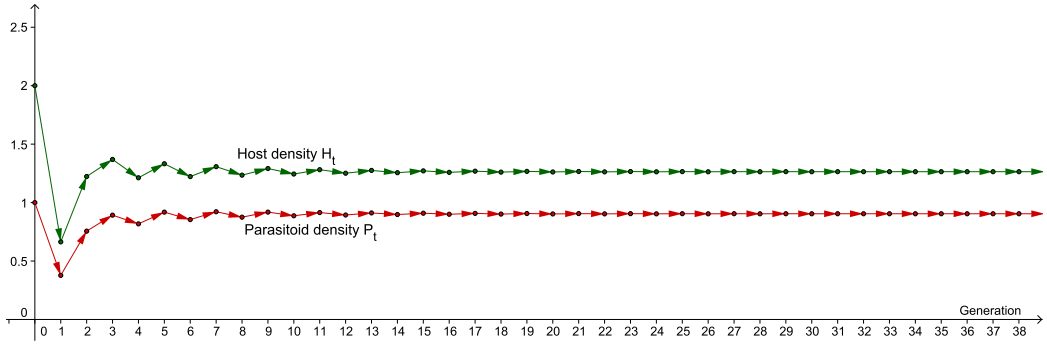



Fig. 14: The parameters are given by $a = 4.7$, $c = 0.3$, $d = 4.1$, $k = 0.43$, $\lambda = 4.55$, $\omega = 2.1$. The initial conditions are $H_0 = 2$ and $P_0 = 1$. From generation $t = 25$ onwards, the host density $H_t$ stays at a value of 1.26 while the parasitoid density $P_t$ stays at 0.9 from generation $t = 25$ on.

[56] cf. Theorem 3.2.1. 2.b)

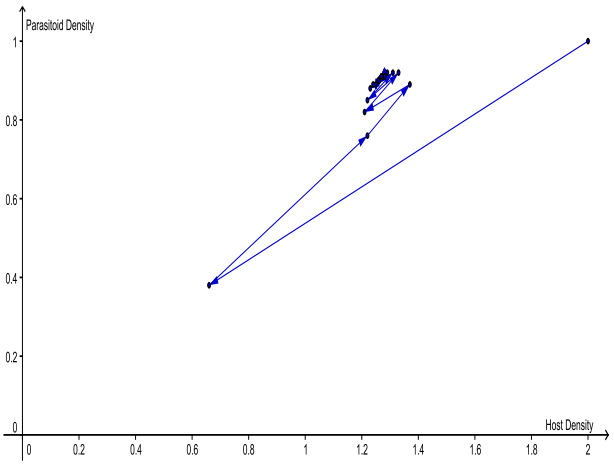



Fig. 15: This figure shows the corresponding phase diagram. The dynamics are converging to the fixed point $(1.26, 0.9)$.

For growing $k$ the dynamics of (12) finally converge towards zero, both species become extinct.[57]

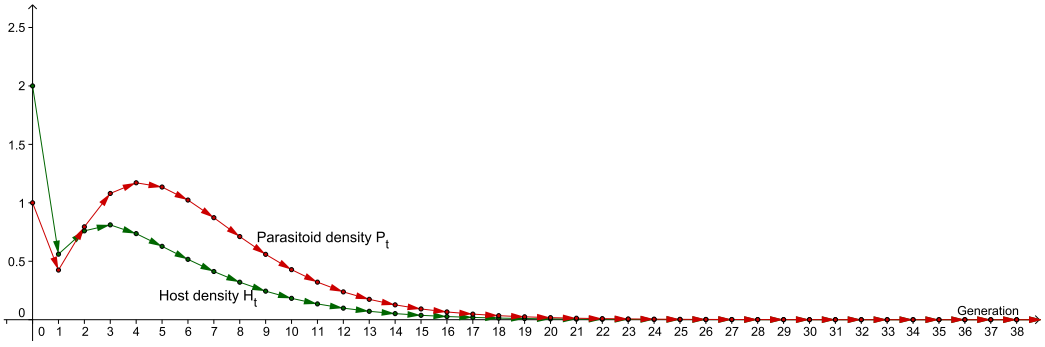



Fig. 16: The parameters are given by $a = 4.7$, $c = 0.3$, $d = 4.1$, $k = 0.62$, $\lambda = 4.55$, $\omega = 2.1$. The initial conditions are $H_0 = 2$ and $P_0 = 1$. Up from generation $t = 23$ and $t = 26$, respectively, the host density $H_t$ and the parasitoid density $P_t$ stay at 0.

[57] cf. Theorem 3.2.1. 2a)

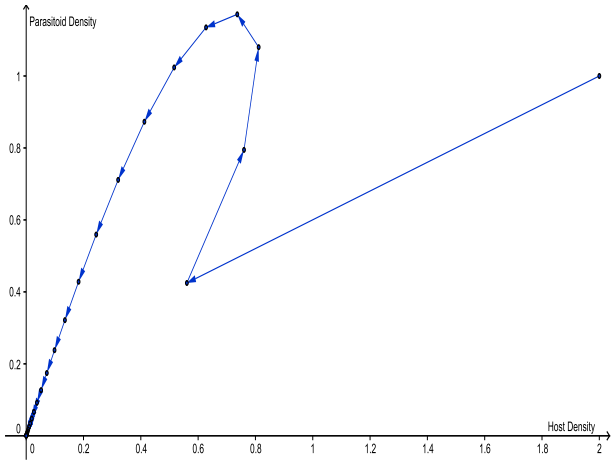



Fig. 17: This figure shows the corresponding phase diagram. The dynamics are converging towards $(0, 0)$.

*Proof:*[58]

The first step is the transformation of the variables $H_t$ and $P_t$ to $H_t = x_t$ and to $\frac{P_t}{H_t} = y_t$ for $H_t > 0$. In this coordinate system the dynamics of (10), (11),

$$\begin{aligned} H_{t+1} &= \lambda H_t g(H_t) f(H_t) \\ P_{t+1} &= \omega H_t (1 - g(\tfrac{P_t}{H_t})) f(H_t) \end{aligned}$$

become partially uncoupled:

The equation describing the host species' density becomes

$$x_{t+1} = \lambda x_t f(x_t) g(y_t). \tag{13}$$

For the derivation of $y_{t+1}$ we start by dividing equation (11) by $H_{t+1}$, whereas $H_{t+1}$ is assumed to be greater than zero. This yields

$$\frac{P_{t+1}}{H_{t+1}} = \omega \frac{H_t}{H_{t+1}} f(H_t) \left(1 - g\left(\frac{P_t}{H_t}\right)\right). \tag{14}$$

Now replace $H_{t+1}$ by $x_{t+1}$ and $\frac{P_{t+1}}{H_{t+1}}$ by $y_{t+1}$. Hence, (14) transforms to

$$y_{t+1} = \omega \frac{x_t}{x_{t+1}} f(x_t)(1 - g(y_t)). \tag{15}$$

With the help of equation (13) the term $f(x_t)$ can be written as $f(x_t) = \frac{x_{t+1}}{\lambda x_t g(y_t)}$. Replace $f(x_t)$ by this expression in equation (15). This yields

$$y_{t+1} = \omega \frac{x_t}{x_{t+1}} \frac{x_{t+1}}{x_t} \frac{1}{\lambda} \left(\frac{1}{g(y_t)} - 1\right). \tag{16}$$

And finally, equation (16) reduces to

$$y_{t+1} = G(y_t) \tag{17}$$

[58] Schreiber 2006, pp. 722-725

where

$$G(y) := \frac{\omega}{\lambda}\left(\frac{1}{g(y)} - 1\right).$$

Furthermore, note that $x_{t+1} = 0 = y_{t+1}$ whenever $x_t = 0$ because we defined $H_{t+1} = 0 = P_{t+1}$ whenever $H_t = 0$.[59] The fact that $g$ is monotonically decreasing, as it was described in the beginning of section 3.2, yields that $G(y)$ is an increasing function and that every solution $y_t$ of (17) converges to a fixed point, possibly $+\infty$ , of $G$. For example, $y = 0$ is always a fixed point of $G$ because

$$G(0) = \frac{\omega}{\lambda}\left(\frac{1}{g(0)} - 1\right) = \frac{\omega}{\lambda}\left(\frac{1}{1} - 1\right) = 0.$$

Further, $G$ is concave for $k < 1$ and convex for $k \geq 1$. This is easy to see with the help of the second derivative of $G(y)$. We get

$$\frac{d^2G(y)}{dy^2} = \frac{a^2(k-1)\left(1 + \frac{ay}{k}\right)^{k-2}\omega}{k\lambda} = \begin{cases} < 0 & \text{for } k < 1 \text{ and all } y \geq 0 \\ \geq 0 & \text{for } k \geq 1 \text{ and all } y \geq 0. \end{cases}$$

For the special case where $k = \infty$ and $g(y) = \exp(-ay)$ the second derivative is given by

$$\frac{d^2G(y)}{dy^2} = \frac{a^2\exp(ay)\omega}{\lambda} > 0$$

for all $y \geq 0$.

[59] See section 3.1.

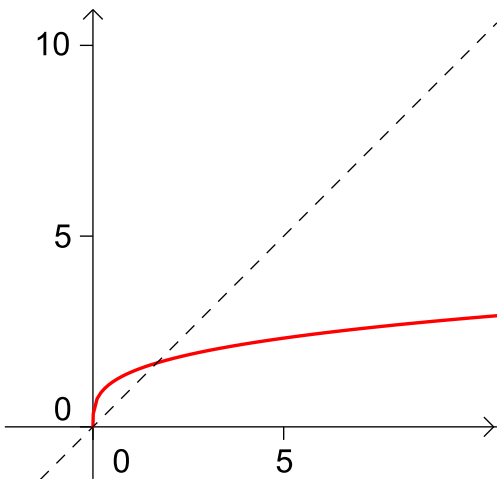



Fig. 18: $k < 1$

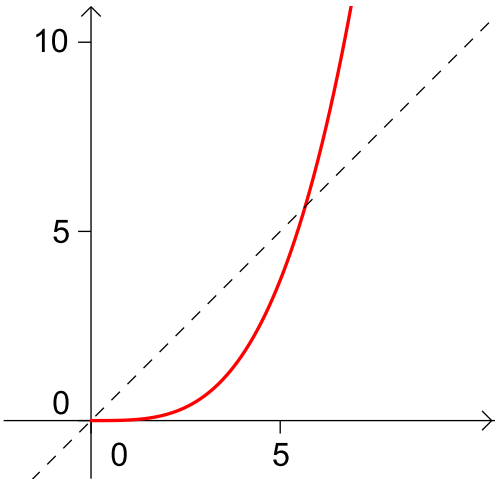



Fig. 19: $k \geq 1$

In order to proceed with the proof, the following lemma is introduced and proven first:[60]

**Lemma 3.2.2.**
*Let $\lambda > 0$. Suppose $y_t$ is a solution to (17) and $y^* := \lim_{t\to\infty} y_t$, possibly $+\infty$.*

1. *If $\lim_{t\to\infty} \lambda g(y_t) < 1$, then*

$$\lim_{t\to\infty} x_t = 0$$

   *for any solution $x_t$ to (13) with $x_0 \geq 0$.*

2. *If $\lim_{t\to\infty} \lambda g(y_t) > 1$, then there exists $M > 0$ such that*

$$\liminf_{t\to\infty} x_t \geq M$$

   *for any solution $x_t$ to (13) with $x_0 > 0$.*

[60] Schreiber 2006, pp. 723 f.

*Proof:*[61]

Let $y_t$ be a solution to (17) and define $y^* := \lim_{t\to\infty} y_t$ and $g^* := g(y^) = \lim_{t\to\infty} g(y_t)$. The expression $g^*$ is well defined since $g$ is continuous.

First, suppose $\lambda g^* < 1$.
Choose $\varepsilon > 0$ sufficiently small so that

$$\rho := \lambda(g^* + \varepsilon) < 1.$$

There exists a $T > 0$ such that $\lambda g(y_t) \leq \rho$ for all $t \geq T$. This follows directly from the convergence of $g(y_t)$ and the triangular inequality:
For all $\varepsilon$ greater than zero there exists $T$ greater or equal to zero such that

$$\mid g^* - g(y_t) \mid \leq \varepsilon \ \forall t \geq T. \tag{18}$$

Inequality (18) implies

$$\mid \lambda g^* - \lambda g(y_t) \mid \leq \lambda\varepsilon \ \forall t \geq T. \tag{19}$$

Now apply the triangular equality to expression (19). This yields

$$-\mid \lambda g^* \mid + \mid \lambda g(y_t) \mid \leq \lambda\varepsilon \ \forall t \geq T,$$

which finally implies

$$\mid \lambda g(y_t) \mid \leq \lambda(g^* + \varepsilon) = \rho.$$

Since $f(x_t) \leq 1$ for all $t$, we have

$$x_{t+1} = \underbrace{\lambda g(y_t)}_{\leq\rho} x_t f(x_t) \leq \rho x_t \underbrace{f(x_t)}_{\leq 1} \leq \rho x_t < x_t$$

for $t \geq T$. Hence, $\lim_{t\to\infty} x_t = 0$ and statement 1. of the lemma is shown.
In biological terms, this first part of the lemma states that if the product of the reproductive rate and the long-term escaping probability is sufficiently low, the host species goes extinct. The limiting value $g^*$ is small if $y^*$ is large. In other words, this means that the ratio of the parasitoids and the hosts

[61] Schreiber 2006, p. 723 f.

finally becomes sufficiently high, i. e. the density of parasitoids is very high compared to the density of the hosts.

Now, suppose $\lambda g^* > 1$.
Choose $\varepsilon > 0$ sufficiently small so that

$$\varrho := \lambda(g^* - \varepsilon) > 1.$$

Define

$$F_1(x) := \lambda x f(x) \text{ and } F_2(x) := \varrho x f(x).$$

$F_1(x)$ describes the density of population $x$ in absence of parasitism.
By making similar considerations as in the previous case, one can again find some $T_1 > 0$ such that $\lambda g(y_t) \geq \varrho$ for all $t \geq T_1$ because $\lim_{t\to\infty} y_t = y^*$. Since $f$ is continuous and $f(0) = 1$, one can choose $\delta > 0$ such that $\varrho f(x) = \underbrace{\lambda(g^* - \varepsilon)}_{>1} f(x) > 1$ for $x \in [0, \delta]$.
Define

$$\alpha := \inf\{F_2(x) : x > \delta\}.$$

Function $f$ is non-increasing by definition. If $f$ is monotonically decreasing and decreases more quickly than $x$ increases, function $F_2$ will decrease as well for $x \to \infty$. In this case, the infimum of $F_2$ is 0. Otherwise, $\alpha$ is positive.

In order to prove the second statement of the lemma, the two cases $\alpha > 0$ and $\alpha = 0$ are investigated separately.

First, suppose $\alpha > 0$.
Define

$$M := \min\{\alpha, \delta\}.$$

From $\varrho f(x) > 1$ for $x \in [0, \delta]$ follows that $F_2(x) = \varrho f(x)x > x$ for $x \in (0, \delta]$ and thus, $F_2(x) > x$ for $x \in (0, M]$. So since $F_2(x) > x$ for $x \in (0, M]$ and

$$x_{t+1} = \underbrace{\lambda g(y_t)}_{\geq \varrho} f(x_t)x_t \geq \varrho f(x_t)x_t = F_2(x_t) \tag{20}$$

for $t \geq T_1$, we get $x_{t+1} \geq F_2(x_t) > x_t$, i. e. $x_t$ is increasing, for $x_t \in (0, M]$ and

$t \geq T_1$. Hence, there exists $T_2 \geq T_1$ such that $x_{T_2} \in [M, \infty)$. Furthermore, the relation $F_2([M, \infty)) \subset [M, \infty)$ holds.
In order to prove this relation, suppose that there exists $x \in [M, \infty)$ with $F_2(x) \in [0, M)$. First, the case

- $M = \alpha$, i. e. $\alpha \leq \delta$, is treated.
  Now there are two cases to distinguish:
  If $x$ lies in $[\alpha, \delta]$, we have $x < F_2(x)$ since $x < F_2(x)$ holds for $x \in (0, \delta]$ but $F_2(x) \in [0, \alpha)$ by assumption, which implies $F_2(x) < x$.
  If $x$ lies in $(\delta, \infty)$, we get a contradiction to the definition of $\alpha$ because we have $x > \delta$ with $F_2(x) < \alpha$.

Now

- $M = \delta$, i. e. $\delta \leq \alpha$, is investigated.
  So we have the case $x \in [\delta, \infty)$ and $F_2(x) \in [0, \delta)$. If $x = \delta$, we already showed that $F_2(\delta) > \delta$ but this is a contradiction to $F_2(\delta) \in [0, \delta)$.
  Now for $x > \delta$ we have that $F_2(x) < \delta \leq \alpha$ by assumption and this is again a contradiction to the definition of $\alpha$ because we have found some $x > \delta$ with $F_2(x) < \alpha$.

Since for arbitrary $x_t$ there is some $T_2 \geq T_1$ such that $x_{T_2} \in [M, \infty)$ and further on, the relations $F_2([M, \infty)) \subset [M, \infty)$ and $x_{t+1} \geq F_2(x_t)$ for all $t \geq T_1$ hold, one gets $x_t \in [M, \infty)$ for all $t \geq T_2$.

Now the case where $\alpha = 0$ is observed.
$F_2$ is non-negative[62] and continuous by definition. Furthermore, $f$ is positive by assumption T1, in particular it can never assume 0, so $F_2$ is positive for $x > 0$. For that reason, $\alpha = 0$ implies that

$$\lim_{x \to \infty} F_2(x) = \lim_{x \to \infty} \varrho x f(x) = \varrho \lim_{x \to \infty} x f(x) = 0,$$

otherwise, i. e. $\lim_{x \to \infty} F_2(x) = a > 0$, function $F_2$ would have a minimum $\beta > 0$ or $F_2$ would be equal to a positive constant up from some value of

[62] in Schreiber 2006, p. 724: *$F_2$ is positive ...*

$x > \delta$ because of the continuity and positivity of $F_2$ for x $\neq 0$. In the first case, this would imply that $\alpha = \beta > 0$. Particularly, note that we cannot have $f \equiv 1$ in the case of $\alpha = 0$. The interpretation of the case $\alpha = 0$ is just that $f(x)$ decreases more quickly to 0 for $x \to \infty$ than $x$ increases to $\infty$.
Obviously, we have

$$\lim_{x\to\infty} F_1(x) = \lambda \lim_{x\to\infty} xf(x) = 0$$

too for $\alpha = 0$.
Now let

$$x^* := \sup\{x : F_1(x) = x,\ x > 0\}.$$

The set $\{x : F_1(x) = x,\ x > 0\}$ is the set of all positive fixed points of $F_1$. Since

$$F_2(x) = \lambda \underbrace{(g^* - \varepsilon)}_{<1} f(x)x < \lambda f(x)x = F_1(x) \tag{21}$$

for all $x > 0$ and $F_2(x) > x$ for $x \in (0, \delta]$, we get $F_1(x) > x$ for $x \in (0, \delta]$. This relation and the fact that $F_1$ is continuous and that $\lim_{x\to\infty} F_1(x) = 0$ allow us to apply the intermediate value theorem which yields that $x^* \in (\delta, \infty)$. Define

$$\gamma := \max\{F_1(x) : x \in [0, x^*]\}.$$

We get $\gamma \geq x^* > \delta$ because $F_1(x) > x$ for $x \in (0, \delta]$ and $F_1(x^*) = x^*$. Now define

$$\xi := \min\{F_2(x) : x \in [\delta, \gamma + 1]\}$$

and

$$M := \min\{\delta, \xi\}.$$

Because of inequality (21) and $F_1(x) < x$ for $x > x^*$, we have $F_2(x) < F_1(x) < x$ for $x > x^*$ and in particular for $x > \gamma$.
With the help of this result we obtain that $F_1([M, \gamma + 1]) \subset [M, \gamma + 1)$ and $F_2([M, \gamma + 1]) \subset [M, \gamma + 1)$.
A detailed proof for $F_1([M, \gamma + 1]) \subset [M, \gamma + 1)$ is given:

The two cases $M = \delta$ an $M = \xi$ are investigated separately.

- $M = \delta$
  The interval $[\delta, \gamma+1]$ splits up into $[\delta, x^*]$ and $(x^*, \gamma+1]$. We first prove that $F_1(x) < \gamma + 1$ for all $x \in [M, \gamma + 1]$.
  Since for $x \in [\delta, x^*]$ it is known that $\gamma \geq F_1(x)$ by definition of $\gamma$, we get in particular, $F_1(x) < \gamma + 1$ for $x \in [\delta, x^*]$. Now $x \in (x^*, \gamma + 1]$. For all $x > x^*$ we have $x > F_1(x)$. Since $x \leq \gamma + 1$, we get again $F_1(x) < \gamma + 1$.
  It remains to show that $F_1(x) \geq \delta$ for all $x \in [\delta, \gamma + 1]$. Suppose there is some $x \in [\delta, \gamma + 1]$ such that $F_1(x) < \delta$. Since $F_2(x) < F_1(x)$ for all $x > 0$, this implies $F_2(x) < \delta \leq \xi$. However, this inequality contradicts the definition of $\xi$. Hence, $F_1(x) \geq \delta$ for all $x \in [\delta, \gamma + 1]$.

- $M = \xi$
  The interval $[\xi, \gamma+1]$ splits up into $[\xi, x^*]$ and $(x^*, \gamma+1]$. We first prove that $F_1(x) < \gamma + 1$ for all $x \in [M, \gamma + 1]$.
  We know that $\gamma \geq F_1(x)$ for all $x \in [\xi, x^*]$ which implies that $F_1(x) < \gamma + 1$ for $x \in [\xi, x^*]$. For $x \in (x^*, \gamma + 1]$ we have $\gamma + 1 \geq x > F_1(x)$.
  In order to get $F_1(x) \geq \xi$ for all $x \in [\xi, \gamma + 1]$ we remember that $F_2(x) > x$ for $x \in (0, \delta]$. In special we obtain $F_2(x) > x$ for all $x \in [\xi, \delta)$. Since $F_1(x) > F_2(x)$, one gets $F_1(x) > x$ and therefore, $F_1(x) > \xi$ for $x \in [\xi, \delta)$. It remains to show that $F_1(x) \geq \xi$ for $x \in [\delta, \gamma+1]$. In order to do so, we assume that there is some $x \in [\delta, \gamma+1]$ such that $F_1(x) < \xi$. Since $F_2(x) < F_1(x)$, we get that $F_2(x) < \xi$ for $x \in [\delta, \gamma + 1]$ but that contradicts the definition of $\xi$. Hence, $F_1(x) \geq \xi$ for $x \in [\delta, \gamma + 1]$.

A detailed proof for $F_2([M, \gamma + 1]) \subset [M, \gamma + 1)$ is provided:
Again the two cases $M = \delta$ an $M = \xi$ are investigated separately.

- $M = \delta$
  Suppose there is some $x \in [\delta, \gamma+1]$ such that $F_2(x) < \delta$. Since $\delta$ is less than $\xi$ by assumption, this contradicts the definition of $\xi$. Therefore,

it remains to show that $F_2(x) < \gamma + 1$ for arbitrary $x \in [\delta, \gamma + 1]$. Since $F_1([M, \gamma + 1]) \subset [M, \gamma + 1)$ is valid and $F_2(x) < F_1(x)$ for all $x$, we get $F_2(x) < \gamma + 1$ for $x \in [M, \gamma + 1]$.

- $M = \xi$
  In order to show $F_2(x) \geq \xi$ for all $x \in [\xi, \gamma + 1]$, assume that there exists some $x \in [\xi, \gamma + 1]$ such that $F_2(x) < \xi$. For $x \in [\delta, \gamma + 1]$ this implies a contradiction to the definition of $\xi$. From $F_2(x) > x$ for $x \in [\xi, \delta)$ follows that $F_2(x) > \xi$ but this contradicts the assumption that $F_2(x) < \xi$. The fact that $F_2(x) < \gamma + 1$ for all $x \in [\xi, \gamma + 1]$ follows again from $F_1([M, \gamma + 1]) \subset [M, \gamma + 1)$ and from $F_2(x) < F_1(x)$ for all $x$.

Note that

$$x_{t+1} = \lambda x_t f(x_t) \underbrace{g(y_t)}_{\leq 1} \leq \lambda f(x_t) x_t = F_1(x_t) \tag{22}$$

holds for all $t \geq 0$. The combination of inequalities (20), (21) and (22) yields

$$F_2(x_t) \leq x_{t+1} \leq F_1(x_t)$$

for all $t \geq T_1$. Hence, we get that if $x_{T_2} \in [M, \gamma + 1]$ for some $T_2 \geq T_1$ ,then $x_t \in [M, \gamma + 1]$ for all $t \geq T_2$. Consequently, in both cases, $\alpha > 0$ and $\alpha = 0$, we have found the positive constant of statement 2. of the lemma.
It remains to show that there exists such a $T_2 \geq T_1$.
If $x_{T_1} \in [M, \gamma + 1]$, then define $T_2 = T_1$.
Now suppose $x_{T_1} \in (0, M)$. Since $F_2(x) > x$ for $x \in (0, \delta]$, we also have $F_2(x) > x$ for $x \in (0, M]$. Moreover, since $F_1(x) \leq \gamma$ holds for all $x \in [0, x^*]$, we have in particular $F_1(x) \leq \gamma$ for $x \in (0, M)$ because $\delta < x^*$ and hence, $M < x^*$.
Suppose $x_t \in (0, M)$. From

$$(0, M) \ni x_t < F_2(x_t) \leq x_{t+1} \leq F_1(x_t) \leq \gamma \in [M, \gamma + 1]$$

for $t \geq T_1$, as it has been already shown, one can conclude that for $x_{T_1} \in (0, M)$ there exists some $T_2 > T_1$ such that $x_{T_2} \in [M, \gamma + 1]$.

Finally suppose $x_{T_1} \in (\gamma+1, \infty)$. If we combine the following results: $F_1(x) < x$ for $x > \gamma$ and $x_{t+1} \leq F_1(x_t)$ for all $t$, we get $x_{t+1} \leq F_1(x_t) < x_t$ for $x_t \in (\gamma+1, \infty)$. So one can find some $T_3 > T_1$ such that $x_{T_3}$ in $(0, \gamma+1)$ if $x_{T_1} \in (\gamma+1, \infty)$. If $x_{T_3} \in [M, \gamma+1]$, the proof is done. If $x_{T_3}$ lies in $(0, M)$ we have the case that was already investigated above and we can therefore apply the preceding arguments to get a $T_2 > T_3$ such that $x_{T_2} \in [M, \gamma+1]$.

□

With the help of this lemma, one can prove the statements of Theorem 3.2.1.[63]

Let us start by considering

1. $\lambda < 1$.
   Let $(x_t, y_t)$ be a solution to the transformed system (13), (17). The given initial conditions $H_0 > 0$ and $P_0 \geq 0$ change to $x_0 > 0$ and $y_0 \geq 0$. It is easy to see that under the given assumptions $\lim_{t\to\infty} x_t = 0$ because we have $f(x) \leq 1$ and $g(x) \leq 1$ for all $x \geq 0$ and hence,

   $$x_{t+1} = \lambda x_t \underbrace{f(x_t)}_{\leq 1} \underbrace{g(x_t)}_{\leq 1} \leq \underbrace{\lambda}_{<1} x_t < x_t$$

   for all $t \geq 0$.
   Further on, since

   $$P_{t+1} = \omega H_t \underbrace{f(H_t)}_{\leq 1} \underbrace{\left(1 - g\left(\frac{P_t}{H_t}\right)\right)}_{\leq 1} \leq \omega H_t = \omega x_t$$

   for all $t \geq 0$, we conclude $\lim_{t\to\infty} P_t = 0$ as well. So the case concerning host failure is done.
   Next, we will investigate what happens for

2. $\lambda > 1$ and $\omega a > \lambda$.
   First suppose $k \geq 1$.
   Again let $(x_t, y_t)$ be a solution to (13), (17). The initial conditions

[63] Schreiber 2006, pp. 724 f.

$H_0 > 0$ and $P_0 > 0$ are transformed to $x_0 > 0$ and $y_0 > 0$.
Since $G(y)$ is convex if $k \geq 1$, $G(0) = 0$ and

$$G'(0) = -\frac{\omega}{\lambda} g'(0) = -\frac{\omega}{\lambda}(-a) = \frac{\omega a}{\lambda} > 1$$

because of $\omega a > \lambda$, we get $G(y) > y$ for $y > 0$. Hence, $y_t$ is increasing and $\lim_{t\to\infty} y_t = \infty$. Since $y_t \to \infty$ and because the continuity of $g$ implies $g(y_t) \to g(\infty) = 0$ for $t \to \infty$, we get $\lim_{t\to\infty} \lambda g(y_t) = \lambda \lim_{t\to\infty} g(y_t) = 0$ and we can therefore apply statement 1. of Lemma 3.2.2., which yields $\lim_{t\to\infty} x_t = 0$ in this case.
Now suppose $k < 1$.
In this case we have

$$\lim_{y\to\infty} \frac{G(y)}{y} = \lim_{y\to\infty} \frac{\frac{\omega a(1+\frac{ay}{k})^{k-1}}{\lambda}}{1} = 0,$$

whereas the rule of de L'Hospital and the observation that $k - 1 < 0$ were applied. Hence, $y$ converges to $\infty$ more quickly than $G(y)$. Since $G$ is concave for $k < 1$, $G'(0) = \frac{\omega a}{\lambda} > 1$ and $\lim_{y\to\infty} \frac{G(y)}{y} = 0$ we conclude that $G(y)$ has a positive fixed point $y^*$, i. e. $y^*$ fulfills $G(y^*) = y^*$. We even get that $y^*$ is uniquely determined by the concavity of $G$. More precisely, we have $G(y) > y$ for $0 < y < y^*$ (because the gradient in 0 is greater than 1) and $G(y) < y$ for $y > y^*$. So since $y_t = G(y_{t-1})$ is monotonically increasing for $0 < y_t < y^*$ and bounded by $y^*$, there exists $c > 0$ such that $y_t$ converges towards $c$ as $t$ goes to $\infty$. Formally, we get

$$\begin{array}{ccc} y_{t+1} & \longrightarrow & c \\ \| & & \\ G(y_t) & \longrightarrow & G(c) \end{array}$$

This yields that $c = G(c)$, i. e. $c$ is a fixed point of $G$, but as was stated earlier, $y^*$ is the only positive fixed point of $G(y)$. Hence, $c = y^*$. The same result is obtained for $G(y)$ with $y > y^*$ in an analogous way: $y_t$ is again a monotone (this time decreasing), bounded sequence that

therefore converges to some $d \geq y^* > 0$. By applying the preceding arguments, we get that $d = y^*$. So the overall result is:

$$\lim_{t\to\infty} y_t = y^*$$

.

Now we will proceed by taking a closer look at the two different cases where $\lambda g(y^*) > 1$ on the one hand, and where $\lambda g(y^*) < 1$ on the other hand.
In the first case, Lemma 3.2.2. implies that there exists $M > 0$ (independent of $x_0$ and $y_0$) such that

$$\liminf_{t\to\infty} x_t = \liminf_{t\to\infty} H_t \geq M$$

. Because of $y_t = \frac{P_t}{H_t}$ we get $\liminf_{t\to\infty} P_t \geq My^* > 0$.
For the second case, Lemma 3.2.2. yields that $\lim_{t\to\infty} x_t = \lim_{t\to\infty} H_t = 0$. Consequently, $\lim_{t\to\infty} P_t = 0$ as well because $P_{t+1} \leq \omega x_t$ for all $t \geq 0$.
Now we want to find the critical value $k = k^*$. It has already been shown that for $k < 1$ there exists a uniquely determined fixed point $y^* > 0$ for $G(y)$. So for any $k \in (0, 1)$ let $y^*(k)$ denote the unique positive fixed point (dependent on $k$) of $G(y)$. In order to determine $k^*$ we start by showing that $G(y)$ is an increasing function of $k$ for arbitrary $y > 0$:

$$\begin{aligned}
\tfrac{dG}{dk} &= \tfrac{\omega}{\lambda}\exp(k\ln(1+\tfrac{ay}{k}))[k\tfrac{1}{1+\frac{ay}{k}}(\tfrac{-ay}{k^2}) + \ln(1+\tfrac{ay}{k})] \\
&= \tfrac{\omega}{\lambda}(1+\tfrac{ay}{k})^k[-\tfrac{ay}{k(1+\frac{ay}{k})} + \ln(1+\tfrac{ay}{k})] \\
&= \tfrac{\omega}{\lambda}\tfrac{(1+\frac{ay}{k})^k h(y)}{k+ay}
\end{aligned}$$

where $h(y) = -ay + (k + ay)\ln(1 + \frac{ay}{k})$. Hence, the sign of $\frac{dG(y)}{dk}$ is determined by the sign of $h(y)$ because the other factors are obviously positive. Therefore, $h(y)$ has to be further analyzed:

It is easy to see that $h(0) = 0$ and that

$$\begin{aligned} h'(y) &= (-a) + a\ln(1+\tfrac{ay}{k}) + (k+ay)\tfrac{1}{\frac{k+ay}{k}}\tfrac{a}{k} \\ &= -a + a\ln(1+\tfrac{ay}{k}) + a \\ &= a\ln(1+\tfrac{ay}{k}) > 0 \end{aligned}$$

for all $y > 0$. So we get $h(y) > 0$ for all $y > 0$ and hence, $\frac{dG}{dk}$ is positive for $y > 0$, i. e. $G(y)$ is increasing in $k$. With this result and the concavity of $G$ for $k < 1$, we get that $y^*(k)$ is an increasing function of $k \in (0, 1)$ as well:

Suppose $k_1 < k_2 < 1$ with $G_{k_1}(y^*(k_1)) = y^*(k_1)$ and $G_{k_2}(y^*(k_2)) = y^*(k_2)$. Since $G$ is a monotonically increasing function in $k$, we get that

$$G_{k_1}(y^*(k_2)) < G_{k_2}(y^*(k_2)) = y^*(k_2).$$

This implies that $G_{k_1}(y^*(k_2))$ lies beneath the 45°-line. By concavity of $G$ for $k < 1$ we obtain that

$$y^*(k_1) < y^*(k_2).$$

Hence, fixed point $y^*(k)$ is monotonically increasing in $k < 1$.

Further investigations show that $y^*(k) \to 0$ as $k \to 0$ and $y^*(k) \to \infty$ as $k \to 1$ since we have

$$G(y) \to 0 \text{ as } k \to 0 \text{ for each } y > 0$$

and

$$G(y) \to \frac{\omega a}{\lambda} y > y \text{ as } k \to 1 \text{ for each } y > 0.$$

Now we are ready to prove the remaining part of the second statement of this theorem:
We know:
Function $g$ is continuous, $g(0) = 1$ and $\lim_{y\to\infty} g(y) = 0$. These properties imply that $\lambda g(0) = \lambda > 1$ (due to assumption) and that

$\lim_{y\to\infty} \lambda g(y) = 0$. Further on, these results and the results about the convergence of $y^*(k)$ yield that $\lim_{k\to 0} g(y^*(k)) = 1$ and $\lim_{k\to 1} g(y^*(k)) = 0$, so there exists a $k^* \in (0,1)$ such that $\lambda g(y^*(k)) > 1$ for $k \in (0, k^*)$ and $\lambda g(y^*(k)) < 1$ for $k \in (k^*, 1)$. Hence, the second statement of Theorem 3.2.1. is proven.
The third statement of Theorem 3.2.1. exhibits the conditions

3. $\lambda > 1$, $\omega a < \lambda$ and $k \leq 1$.
   Let $(x_t, y_t)$ be a solution to the system (13), (17) such that $x_0 > 0$ and $y_0 \geq 0$ which is equivalent to $H_0 > 0$ and $P_0 \geq 0$.

   Remember that $G(0) = 0$, further $G'(0) = \frac{\omega a}{\lambda} < 1$ in this case. This investigation and the concavity of $G$ enhance that $y_{t+1} = G(y_t) < y_t$ for all $y_t > 0$. Therefore, $\lim_{t\to\infty} y_t = 0$. Again we use the continuity of $g$ and that $g(y_t) \to 1$ for $y_t \to 0$ to receive $\lim_{t\to\infty} \lambda g(y_t) = \lambda > 1$ in this very case. So we can apply Lemma 3.2.2 that guarantees us that there exists $M > 0$ (independent of $x_0$ and $y_0$) such that $\liminf_{t\to\infty} x_t \geq M$.
   The last statement of Theorem 3.2.1. concerns the case where

4. $\lambda > 1$, $\omega a < \lambda$ and $k > 1$.
   Let $(x_t, y_t)$ denote a solution to the system (13), (17) with $x_0 > 0$ and $y_0 > 0$, what corresponds to $H_0 > 0$ and $P_0 > 0$ of the original system. Since $G(y)$ is convex for $k \geq 1$, $G'(0) = \frac{\omega a}{\lambda} < 1$ and

$$\lim_{y\to\infty} \frac{G(y)}{y} = \lim_{y\to\infty} \frac{\omega a (1 + \frac{ay}{k})^{k-1}}{\lambda} = \infty,$$

   i. e. $G(y)$ will finally run above the 45°-line and stay there, there exists a uniquely determined positive fixed point $y^*$ of $G(y)$. Because of the convexity of $G$ we even get that $G(y) < y$ for $y < y^*$ and $G(y) > y$ whenever $y > y^*$, i. e. $y_t$ is increasing as $t$ increases whenever $y_0 > y^*$. So we conclude that $\lim_{t\to\infty} y_t = \infty$ if we assume $y_0 > y^*$, which is equivalent to

$$0 < y^* < \frac{P_0}{H_0}. \tag{23}$$

   Inequality (23) can be rewritten as

$$0 < y^* H_0 < P_0.$$

Again we can refer to Lemma 3.2.2. because the result we just obtained implies that $\lim_{t\to\infty} \lambda g(y_t) = 0 < 1$ and therefore, we get that $\lim_{t\to\infty} x_t = 0$.
Since $P_{t+1} \leq \omega x_t$ for all $t$, we get $\lim_{t\to\infty} P_t = 0$ as well.
Now suppose $y_0 < y^*$. We can transform the initial condition

$$0 \leq \frac{P_0}{H_0} < y^* \tag{24}$$

to

$$0 \leq P_0 < y^* H_0$$

as it is found in statement 4. of Theorem 3.2.1. Then $y_t$ is decreasing and we get $\lim_{t\to\infty} y_t = 0$. This implies $\lim_{t\to\infty} \lambda g(y_t) = \lambda > 1$ and hence, we can find some $M > 0$ such that $\liminf_{t\to\infty} x_t \geq M$.
Finally, note that because $G$ is convex and increasing with respect to $k$,[64] $y^*(k)$ decreases as $k > 1$ increases:

Suppose $1 < k_1 < k_2$ with $G_{k_1}(y^*(k_1)) = y^*(k_1)$ and $G_{k_2}(y^*(k_2)) = y^*(k_2)$. Since $G$ is a monotonically increasing function in $k$, we get that

$$G_{k_1}(y^*(k_2)) < G_{k_2}(y^*(k_2)) = y^*(k_2).$$

This implies that $G_{k_1}(y^*(k_2))$ lies beneath the 45°-line. By convexity of $G$ for $k > 1$ we obtain that

$$y^*(k_1) > y^*(k_2).$$

Hence, fixed point $y^*(k)$ is monotonically decreasing in $k > 1$.

□

[64] See analysis in part 2. of the proof.

# 4 Detailed Analysis of the Thompson Model

Let $H$ and $H'$ denote the host density of the present generation and the host density of the following generation, respectively. Analogously, let $P$ and $P'$ denote the present density of the parasitoid species and the density of the next generation, respectively.

## 4.1 The Original Thompson Model

This subsection is devoted to a detailed analysis of the original Thompson model[65]

$$H' = \lambda H g\left(\frac{P}{H}\right) \tag{25}$$

$$P' = H\left(1 - g\left(\frac{P}{H}\right)\right) \tag{26}$$

where $g(x) = \exp(-ax)$.
It will be shown that the Thompson model has no positive fixed point at all except for the case where $a$ fulfills some special condition. Otherwise, the dynamics of the original Thompson model either go to 0, i. e. the parasitoid species drives the host to extinction, or the dynamics go to infinity, i. e. the host species escapes from parasitism and both species grow unchecked depending on the initial conditions and on the parameters $a$ and $\lambda$.[66]
The following two figures show these completely different dynamics described above. Note that just the initial values for the population densities are shifted.

[65] Thompson 1924, pp. 69-89
[66] Hassell 2000, p. 11

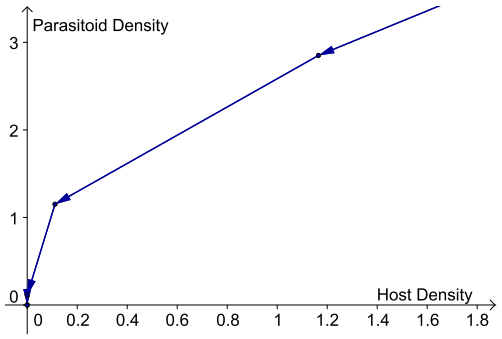



Fig. 20: The parameters are given by $a = 1.8$, $\lambda = 7.8$; $H_0 = 3$; $P_0 = 5$

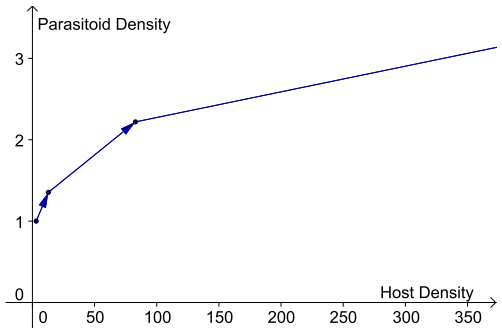



Fig. 21: The parameters are given by $a = 1.8$, $\lambda = 7.8$; $H_0 = 1$; $P_0 = 1$

### 4.1.1 Computation of the Isoclines and Fixed Point(s)

Let us first introduce a general definition of a nullcline or isocline of a discrete system:

The $x_i$-isocline of an $n$-dimensional system

$$x_i' = f_i(x_1, \ldots, x_n)$$

for $i = 1, \ldots, n$ is defined as

$$x_i\text{-isocline} := \{(x_1, \ldots, x_n) \in \mathbb{R}_+^n : f_i(x_1, \ldots, x_n) = x_i\}.$$

Now apply this definition to the system of interest in order to find out about its dynamical behaviour.

The $H$-isocline is given by:

$$\begin{array}{rcccccl} & H & = & \lambda H \exp\left(-\frac{aP}{H}\right) & & & \\ \Leftrightarrow & H & = & 0 & \text{or} & 1 & = \lambda \exp\left(-\frac{aP}{H}\right) \\ & & & & \Leftrightarrow & \exp\left(\frac{aP}{H}\right) & = \lambda \\ & & & & \Leftrightarrow & \frac{aP}{H} & = \ln \lambda \\ & & & & \Leftrightarrow & P & = H\frac{\ln \lambda}{a} \end{array}$$

The $P$-isocline is given by:

$$\begin{array}{rcccccl} & P & = & H\left(1-\exp\left(-\frac{aP}{H}\right)\right) & & & \\ \Leftrightarrow & P & = & 0 & \text{or} & P & = H\left(1-\exp\left(-\frac{aP}{H}\right)\right) \end{array}$$

One fixed point of the system (25), (26) is obviously the point $(H_0^*, P_0^*) = (0,0)$. However, in order to find a possible positive fixed point, the intersection point of the two isoclines will be calculated. Suppose that $\lambda > 1$, otherwise Theorem 3.2.1. yields $\lim_{t\to\infty}(H_t, P_t) = 0$ for any initial condition $H_0 > 0$, $P_0 \geq 0$. Without using the theorem the dynamics of the system for $\lambda < 1$ can also be seen by the following estimates,

$$H' \leq \lambda H \Rightarrow H_t \to 0 \text{ as } t \to \infty$$

$$P' \leq H \Rightarrow P_t \to 0 \text{ as } t \to \infty.$$

So for $\lambda < 1$ there exists just one fixed point, $(H_0^*, P_0^*) = (0,0)$, which is attracting and stable. Hence, it is asymptotically stable.

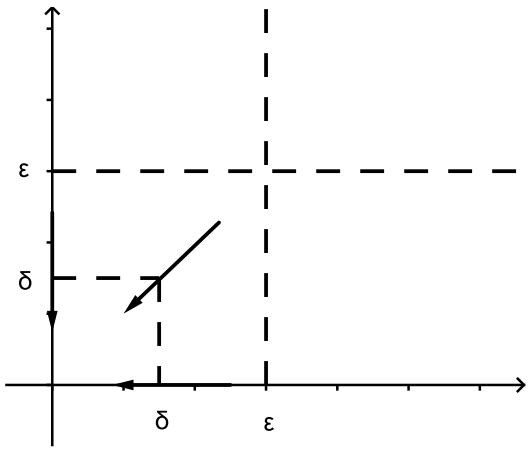



Fig. 22: A solution starting in the $\delta$-region cannot leave the $\varepsilon$-region (not even the $\delta$-region) since $H' < H$ and $P' < H$ for $\lambda < 1$. This implies that $(H_0^*, P_0^*)$ is stable.

For $\lambda > 1$ this equilibrium is unstable since $H_t \to \infty$ as $t \to \infty$ if $H_0 > 0$ and $P_0 = 0$. In biological terms, this means that in the absence of parasitism the host population will grow exponentially.

Now, we want to find out if there are any positive fixed points in addition to the origin:

By intersecting the $H$- and $P$-isoclines we get:

$$\begin{array}{rccc} & H\frac{\ln\lambda}{a} & = & H(1-\exp(-\frac{aH\frac{\ln\lambda}{a}}{H})) \\ \Leftrightarrow & \frac{\ln\lambda}{a} & = & 1-\exp(-\ln\lambda) \\ \Leftrightarrow & \frac{\ln\lambda}{a} & = & 1-\frac{1}{\lambda} \\ \Leftrightarrow & a & = & \frac{\ln\lambda}{1-\frac{1}{\lambda}} \\ & & = & \frac{\ln\lambda}{\frac{\lambda-1}{\lambda}} \\ & & = & \frac{\lambda\ln\lambda}{\lambda-1} \end{array}$$

Now, plugging in the result for $a$ in the $H$- and $P$-isocline yields

$$P = H\frac{\ln\lambda}{\frac{\lambda\ln\lambda}{\lambda-1}} = H\frac{\lambda-1}{\lambda} = H\left(1-\frac{1}{\lambda}\right)$$

$$P = H\left(1-\exp\left(-\frac{\lambda\ln\lambda}{\lambda-1}\frac{P}{H}\right)\right).$$

In order to calculate possible fixed points under the obtained condition for $a$ we intersect the isoclines again:

$$\begin{array}{rccc} & H(1-\frac{1}{\lambda}) & = & H(1-\exp(-\frac{\lambda\ln\lambda}{\lambda-1}\frac{P}{H})) \\ \Leftrightarrow & 1-\frac{1}{\lambda} & = & 1-\exp(-\frac{\lambda\ln\lambda}{\lambda-1}(1-\frac{1}{\lambda})) \\ \Leftrightarrow & 1-\frac{1}{\lambda} & = & 1-\exp(-\ln\lambda) \\ \Leftrightarrow & 1-\frac{1}{\lambda} & = & 1-\frac{1}{\lambda}. \end{array}$$

As the calculation shows, the $H$- and $P$-isocline completely overlap, i. e. there are infinitely many positive fixed points, if and only if $a = \frac{\lambda\ln\lambda}{\lambda-1}$. Since $\lambda > 1$ and the derivative of this isocline is given by $1-\frac{1}{\lambda}$ its the gradient is between 0 and 1, in particular this isocline cannot cross the 45°-line.

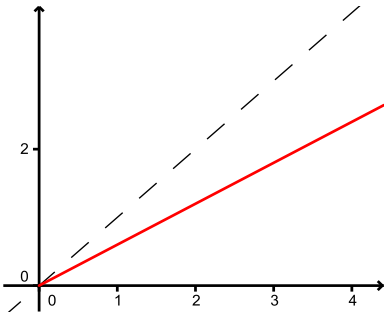



Fig. 23: This figure shows the $H$- and $P$-isocline under the conditions $\lambda = 2.5$ and $a = \frac{\lambda \ln \lambda}{\lambda - 1}$ with the dashed 45°-line.

For $a \neq \frac{\lambda \ln \lambda}{\lambda - 1}$, $(H_0^*, P_0^*) = (0, 0)$ is the only fixed point of the original Thompson model (25), (26).
For $a = \frac{\lambda \ln \lambda}{\lambda - 1}$ and $\lambda > 1$ we have a line of infinitely many fixed points.[67] Since $\lambda > 1$, $\lambda > \omega a = 1 \times \frac{\lambda \ln \lambda}{\lambda - 1}$ and $k = \infty > 1$, Theorem 3.2.4. proves them to be unstable.

## 4.2 The Thompson Model with Aggregated Search

This subsection is devoted to a detailed analysis of a slightly modified Thompson model

$$H' = \lambda H g\left(\frac{P}{H}\right) \tag{27}$$

$$P' = H\left(1 - g\left(\frac{P}{H}\right)\right) \tag{28}$$

where $g(x) = (1 + \frac{ax}{k})^{-k}$ and $k \in (0, \infty)$.[68]
By deriving the $H$- and $P$-isocline and intersecting them we want to find out if this slight modification of the original Thompson model has inner equilibria or not.

[67] Getz & Mills 1996, p. 342; Hassell 2000, p. 11
[68] Getz & Mills 1996, p. 344

### 4.2.1 Computation of the Isoclines and Fixed Point(s)

The $H$-isocline is given by:

$$\begin{array}{rcccccl} & H & = & \lambda H(1+\frac{aP}{kH})^{-k} & & & \\ \Leftrightarrow & H & = & 0 & \text{or} & 1 & = \lambda(1+\frac{aP}{kH})^{-k} \\ & & & & \Leftrightarrow & (1+\frac{aP}{kH})^{k} & = \lambda \\ & & & & \Leftrightarrow & 1+\frac{aP}{kH} & = \lambda^{\frac{1}{k}} \\ & & & & \Leftrightarrow & \frac{aP}{kH} & = \lambda^{\frac{1}{k}}-1 \\ & & & & \Leftrightarrow & P=\frac{\left(\lambda^{\frac{1}{k}}-1\right)kH}{a} & \end{array}$$

The $P$-isocline is given by:

$$\begin{array}{rcccccl} & P & = & H(1-(1+\frac{aP}{kH})^{-k}) & & & \\ \Leftrightarrow & P & = & 0 & \text{or} & P & = H(1-(1+\frac{aP}{kH})^{-k}) \end{array}$$

The point $(H_0^*, P_0^*) = (0,0)$ is an equilibrium of system (27), (28). Possible other fixed points can be found by intersecting the isoclines. Again $\lambda$ is assumed to be greater than 1 because otherwise the dynamics of (27), (28) will go to $(0,0)$ for any initial condition, in particular $(H_0^*, P_0^*) = (0,0)$ is asymptotically stable in the case $\lambda < 1$.[69] This equilibrium is unstable for $\lambda > 1$ since $H_t \to \infty$ as $t \to \infty$ if $H_0 > 0$ and $P_0 = 0$. In other words, this means that in the absence of parasitism the host population will grow exponentially.

So, as was announced before, possible inner fixed points are given by the intersection of the isoclines:

By intersecting the $H$- and $P$-isoclines we get:

$$\begin{array}{rcccl} & \frac{\left(\lambda^{\frac{1}{k}}-1\right)kH}{a} & = & H\left(1-\left(1+\frac{a}{k}\frac{\left(\lambda^{\frac{1}{k}}-1\right)k}{a}\right)^{-k}\right) \\ \Leftrightarrow & \frac{\left(\lambda^{\frac{1}{k}}-1\right)k}{a} & = & 1-\frac{1}{\lambda} \\ \Leftrightarrow & a & = & \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1} \end{array}$$

[69] See the stability analysis of $(H_0^*, P_0^*)$ on page 44.

Now, plugging in the result for $a$ in the $H$- and $P$-isocline yields

$$P = \frac{(\lambda - 1)H}{\lambda} = \left(1 - \frac{1}{\lambda}\right) H$$

$$P = H\left(1 - \left(1 + \frac{\lambda\left(\lambda^{\frac{1}{k}} - 1\right)}{\lambda - 1}\frac{P}{H}\right)^{-k}\right).$$

In order to calculate possible fixed points under the obtained condition for $a$, we intersect the isoclines again. After reducing the terms we see that the isoclines overlap as it is the case with randomly distributed parasitoids.

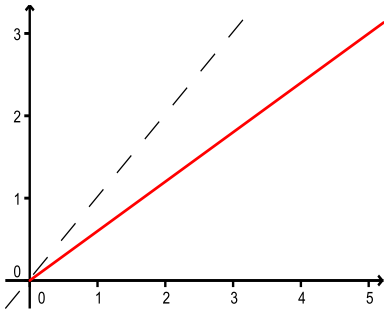



Fig. 24: This figure shows the $H$- and $P$-isocline under the conditions $\lambda = 2.5$ and $a = \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$ with the dashed 45°-line.

The dynamics of (27), (28) with $a = \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$ are easy to see with the help of the following computation:

$$
\begin{array}{rcccc}
H'-H & = & \lambda H\left(1+\frac{aP}{kH}\right)^{-k}-H & < & 0 \\
& \Leftrightarrow & H\left(\lambda\left(1+\frac{aP}{kH}\right)^{-k}-1\right) & < & 0 \\
& \Leftrightarrow & \lambda\left(1+\frac{aP}{kH}\right)^{-k} & < & 1 \\
& \Leftrightarrow & \lambda & < & \left(1+\frac{aP}{kH}\right)^{k} \\
& \Leftrightarrow & \lambda^{\frac{1}{k}} & < & 1+\frac{aP}{kH} \\
& \Leftrightarrow & \underbrace{\frac{\left(\lambda^{\frac{1}{k}}-1\right)kH}{a}}_{H-isocline} & < & P
\end{array}
$$

$$
\begin{array}{rcccc}
P'-P & = & H\left(1-\left(1+\frac{aP}{kH}\right)^{-k}\right)-P & < & 0 \\
& \Leftrightarrow & \underbrace{H\left(1-\left(1+\frac{aP}{kH}\right)^{-k}\right)}_{P-isocline} & < & P
\end{array}
$$

Hence, these computations yield the following plot:

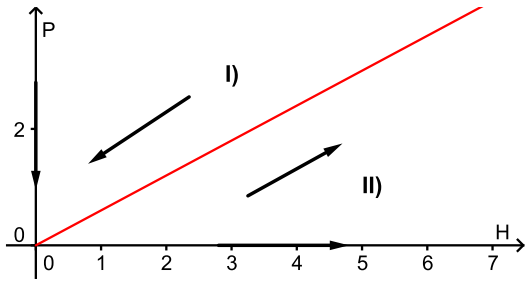



Fig. 25: The parameters are $\lambda = 2.5$ and $a = \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$.

According to the preceding calculations the dynamics in area I) and II) are:

| Quadrant | Dynamic | Biological Meaning |
|---|---|---|
| I) | $H'-H<0$ and $P'-P<0$ $\swarrow$ | The host and the parasitoid population are decreasing. |
| II) | $H'-H>0$ and $P'-P>0$ $\nearrow$ | The host and the parasitoid pop. increase. |

These results also hold for the case where $k = \infty$, i. e. where $g(x) = \exp(-ax)$.

For $a \neq \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$, $(H_0^*, P_0^*) = (0,0)$ is the only fixed point of the Thompson model with aggregated search (27), (28).
For $a = \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$ and $\lambda > 1$ we have a line of infinitely many fixed points. Since $\lambda > 1$ and $\lambda > \omega a = 1 \times \frac{\lambda\left(\lambda^{\frac{1}{k}}-1\right)k}{\lambda-1}$, Theorem 3.2.4. proves them to be unstable for $k > 1$.
So, the overall result of this section is that both the original Thompson model and its slight modification have no positive fixed point at all unless the parameter $a$ fulfills some special condition.[70]
It is not until the introduction of a regulating term for the density of the host species that the Thompson model shows periodic behaviour or a positive fixed point.
Introduce for example

$$H' = \lambda H \left(1 + \frac{aP}{kH}\right)^{-k} \frac{1}{1 + cH_t^d}$$

$$P' = \omega H \left(1 - \left(1 + \frac{aP}{kH}\right)^{-k}\right)$$

Different dynamics of this system are illustrated below:

[70] Hassell 2000, p. 11

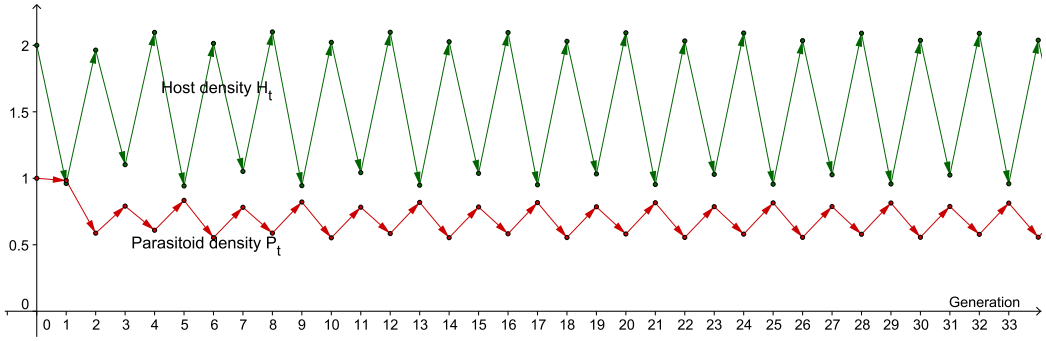



Fig. 26: The parameters are given by $a = 2.7$, $c = 0.3$, $d = 4.1$, $k = 0.22$, $\lambda = 4.55$, $\omega = 1.4$. The initial conditions are $H_0 = 2$ and $P_0 = 1$.

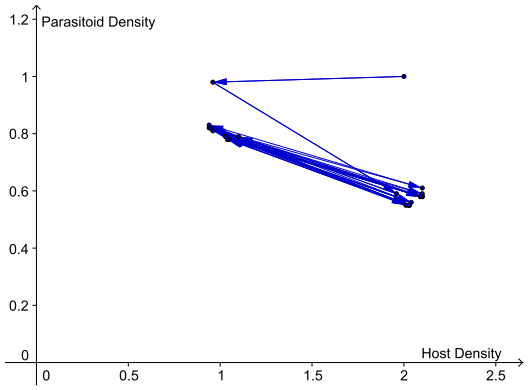



Fig. 27: This figure shows the corresponding phase diagram.

The dynamics of the system above are periodic. However, if on slightly modifies the value of $k$, the system even has a fixed point:

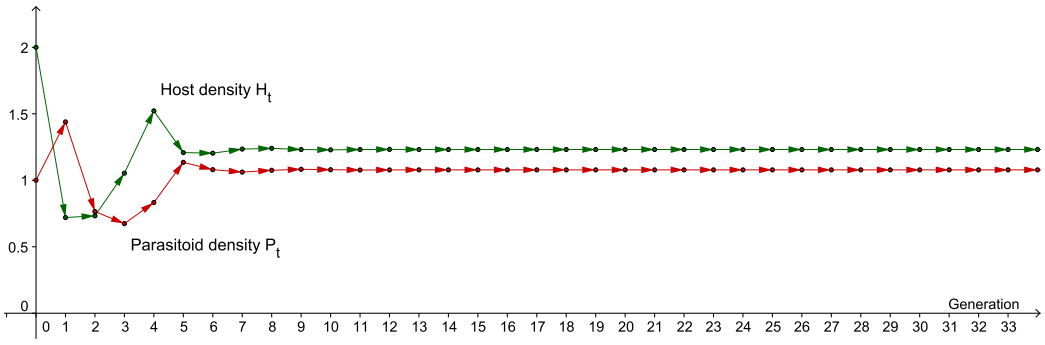



Fig. 28: The parameters are given by $a = 2.7$, $c = 0.3$, $d = 4.1$, $k = 0.63$, $\lambda = 4.55$, $\omega = 1.4$. The initial conditions are $H_0 = 2$ and $P_0 = 1$. The inner equilibrium is at $(1.23, 1.08)$.

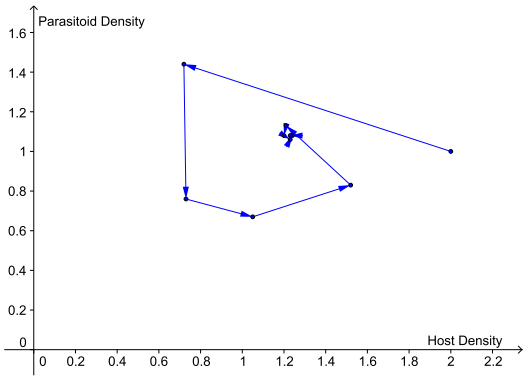



Fig. 29: This figure shows the corresponding phase diagram. The dynamics are converging to the fixed point $(1.23, 1.08)$.

We will see in section 6 that the original Nicholson-Bailey model and its modification exhibit even more interesting dynamics than the Thompson model.

# 5 The Nicholson-Bailey Model

## 5.1 Introduction

The original Nicholson-Bailey model

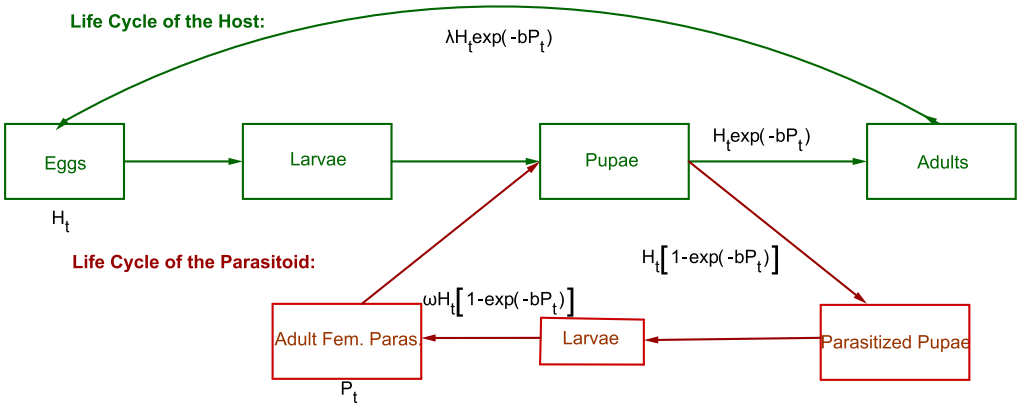
$$\begin{aligned} H_{t+1} &= \lambda H_t g(E) \\ P_{t+1} &= \omega H_t (1 - g(E)) \end{aligned} \tag{29}$$

with $g(E) = \exp(-E)$ was developed by Alexander John Nicholson (entomologist) and Victor Albert Bailey (physician) in 1935.[71] The exact derivation of system (29), the meaning of its parameters and of the escape function $g$ can be found in section 1.1.2. As in the original Thompson model (8), function $g$ is an exponential function. In contrast to the Thompson model, the parasitoid species is not assumed to be egg-limited. Nicholson and Bailey suggested that the parasitoids experience search-limitation. This means that the parasitoids are just limited in their ability to find hosts but not restricted in the number of eggs they can produce. Further on, the average host-parasitoid encounter rate obeys the law of mass action, i. e. the encounter rate is proportional to the product of $H_t$ and $P_t$.[72] Hence, the mean number of host-parasitoid encounters per host is given by

$$E = \frac{bH_tP_t}{H_t} = bP_t \tag{30}$$

where $b$ is the per capita searching efficiency of the parasitoid species.[73]
The following graphic illustrates the original Nicholson-Bailey model (29).

[71] Nicholson & Bailey 1935, pp. 551-598
[72] Elaydi 1999, p. 211; Hassell 2000, p. 14
[73] Getz & Mills, p. 335




While the original Nicholson-Bailey model (29) neglects density-dependent factors influencing the host population's growth, its generalization[74]

$$H_{t+1} = \lambda H_t g(P_t) f(H_t) \tag{31}$$

$$P_{t+1} = \omega H_t \left(1 - g(P_t)\right) \tag{32}$$

with $g(P_t) = \exp(-bP_t)$ and $f(H_t) = \exp(-cH_t)$, includes a density-dependent survival function denoted by $f$ in addition to the escape function $g$.
This special generalization of the Nicholson-Bailey model is known as the Beddington model. It was proposed by J. R. Beddington, J. H. Lawton and C. A. Free.[75] Model (31), (32) has already been derived in section 1.1.2 for arbitrary escape function $g$ and density-dependent survival function $f$. Now, we want to emphasise the explicit forms of $g$ and $f$ of the Beddington model. As in the original Nicholson-Bailey model, Beddington assumed the parasitoid species to be randomly distributed among the host population. Hence, the escape function $g$ is given by $g(P_t) = \exp(-bP_t)$. Further information about the derivation of the escape function $g$ is provided in section 7.
Considering the density-dependent survival function $f$, one realizes that it is given by the Ricker map $f(H_t) = \exp(-cH_t)$. In the absence of parasitoids $f$ acts as density-dependent self-regulation for the host species.[76] It

[74] Kon 2006, p. 173
[75] Beddington et al. 1975, pp. 58-60
[76] Beddington et al. 1975, p. 58

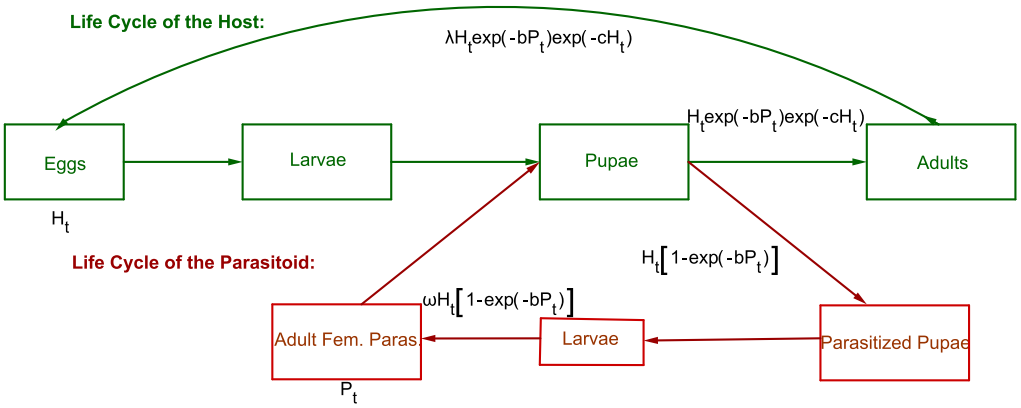
controls the population growth of the host species. Otherwise, if there is no density-dependent function $f$, i. e. in case of

$$H_{t+1} = \lambda H_t,$$

the dynamics of (31) would go to infinity for $\lambda > 1$. Since in nature there are influences that affect the host density, like intra-specific competition or predation, unchecked population growth in absence of the parasitoid species is very unrealistic.[77]

Further on, note that $f$ depends on the initial host density $H_t$ prior to parasitism. The model suggests that mortality due to parasitism precedes mortality caused by density-dependent factors. However, density-dependent mortality is determined by the host density $H_t$ prior to parasitism.

The following graphic illustrates two possible life cycles of a host (green) and a parasitoid (red) species in correlation with the Beddington model (31), (32).




In section 6, we will also treat a model where $g(P_t) = \exp(-bP_t)$ is replaced by $g(P_t) = \left(1 + \frac{bP_t}{k}\right)^{-k}$.

Finally, note that system (31), (32) is defined at the origin in contrast to the generalized Thompson model.

[77] Nicholson & Bailey 1935, p.555

## 5.2 Dynamics of the Generalized Nicholson-Bailey Model - The Beddington Model

This subsection is dedicated to the analysis of system (31), (32)[78]

$$\begin{aligned} H_{t+1} &= \lambda H_t \exp(-bP_t) \exp(-cH_t) \\ \\ P_{t+1} &= \omega H_t \left(1 - \exp(-bP_t)\right). \end{aligned}$$

We will calculate possible fixed points and investigate their stability properties. Moreover, we will focus on boundary cycles.
In order to proceed, system (31), (32) is rescaled by substituting $cH_t$ and $bP_t$ by $x_t$ and $y_t$, respectively, and by introducing new parameters $r = \log \lambda$ and $\theta = \frac{\omega b}{c}$. Both new parameters are greater than zero since $b$, $c$ and $\omega$ are greater than zero and since $\lambda$ is assumed to be greater than one. Consequently, these modifications yield the following rescaled model:[79]

$$x_{t+1} = x_t \exp(r - x_t - y_t) \tag{33}$$

$$y_{t+1} = \theta x_t \left(1 - \exp(-y_t)\right) \tag{34}$$

Equation (33) was obtained by multiplying equation (31) with parameter $c$ on both sides, which gives

$$cH_{t+1} = \lambda cH_t \exp(-bP_t) \exp(-cH_t). \tag{35}$$

Then, use $\exp(r) = \lambda$ and replace the former variables $cH_{t+1}$, $cH_t$ and $bP_t$ in (35) by the new variables introduced above. This gives equation (33).
Equation (34) is obtained in a similar way. First, both sides of equation (32) are multiplied by parameter $b$, which yields

$$bP_{t+1} = \omega bH_t \left(1 - \exp(-bP_t)\right). \tag{36}$$

Now replace $H_t$ by $x_t \frac{1}{c}$. Since $c$ is greater than zero, the expression $x_t \frac{1}{c}$ is well-defined. Hence, equation (36) transforms to

$$bP_{t+1} = \omega b \frac{1}{c} x_t \left(1 - \exp(-bP_t)\right). \tag{37}$$

[78] Beddington et al. 1975, pp. 58-60; Kon 2006, p. 173
[79] Kon 2006, p. 174

Finally, plug in the new variables and parameters into (37). This returns equation (34).

Since the rescaled system (33), (34) just contains 2 parameters in contrast to system (31), (32), that exhibits 4 parameters, the rescaled system (33), (34) is somewhat easier to analyze. We will therefore consider the dynamics and fixed points of system (33), (34).
Possible equilibria of system (33), (34) are obtained by solving the 2-dimensional system

$$x_t = x_t \exp(r - x_t - y_t) \tag{38}$$

$$y_t = \theta x_t \left(1 - \exp(-y_t)\right). \tag{39}$$

The most obvious solution of this system is given by $E_{00} = (0, 0)$. System (38), (39) is also solved by $x_t = r$ and $y_t = 0$. Hence, there is a fixed point on the $x$-axes. It is denoted by $E_{+0} = (r, 0)$. These two equilibria, $E_{00}$ and $E_{+0}$ exist for any given set of parameters.
There exists an inner equilibrium as well, denoted by $E_{++} = (x^*, y^*)$ and given by the unique positive root of[80]

$$r = x^* + y^* \tag{40}$$

$$x^* = \frac{y^*}{\theta \left(1 - \exp\left(-y^*\right)\right)}. \tag{41}$$

Equation (40) was derived by reducing (38) to

$$1 = \exp(r - x_t - y_t). \tag{42}$$

By applying the logarithm to (42), one finally obtains condition (40).
Equation (41) can be derived easily from equation (39).

The positive equilibrium $E_{++} = (x^*, y^*)$ does not always exist. With the help of some straight-forward computations, we will see that $E_{++}$ exists if and only if $\theta r > 1$.[81]

[80] Kon 2006, p. 174

[81] Kon 2006, p. 174; Kon & Takeuchi 2001b, p. 289; Kon and Takeuchi give the conditions for existence and stability of $E_{++}$ in terms of the non-rescaled system. Here, this analysis is done for the rescaled system.

Start by defining function $f$ as

$$f(z) := \frac{z}{\theta\left(1-\exp\left(-z\right)\right)} - (r-z). \tag{43}$$

Note that $f$ is derived from system (40), (41). Or, more exactly spoken, function $f$ is obtained by the difference of the $x$- and $y$-isocline given by

$$x_t = \begin{cases} r - y_t \\ \frac{y_t}{\theta(1-\exp(-y_t))}. \end{cases}$$

Only if $f$ intersects the $x$-axes, i. e. only if there is some $\widetilde{z}$ such that $f(\widetilde{z}) = 0$, the positive fixed point $E_{++}$ does exist. Therefore, we have to take a closer look at the properties of $f$. The properties of $f$ will return that $f$ intersects the abscissa if and only if $\theta r > 1$.
First, the monotony of function $f$ is investigated:

$$\begin{aligned} f'(z) &= \frac{\theta\left(1-\exp\left(-z\right)\right) - z\left(-\theta\exp\left(-z\right)(-1)\right)}{\theta^2\left(1-\exp\left(-z\right)\right)^2} + 1 \\ &= \frac{\theta\left(1-\exp\left(-z\right)\right) - z\theta\exp\left(-z\right)}{\theta^2\left(1-\exp\left(-z\right)\right)^2} + 1 \\ &= \frac{1-\exp\left(-z\right)(1+z)}{\theta\left(1-\exp(-z)\right)^2} + 1 \end{aligned} \tag{44}$$

The derivative of $f$ is greater than zero for all $z$ greater than zero. In fact, we can prove that the numerator of the fraction in (44) is always positive for $z > 0$. We will show that

$$\exp\left(-z\right)(1+z) < 1 \text{ for } z > 0 \tag{45}$$

holds.
Start by defining

$$g(z) := \exp\left(-z\right)(1+z). \tag{46}$$

For $z = 0$ we get

$$g(0) = \frac{1}{\exp(0)} \times 1 = 1.$$

Now we take a look at the limiting case $z \to \infty$, which yields

$$\begin{aligned} \lim_{z\to\infty} g(z) &= \lim_{z\to\infty} \tfrac{1+z}{\exp(z)} \\ &= \lim_{z\to\infty} \tfrac{1}{\exp(z)} \\ &= 0. \end{aligned}$$

As far as monotony is concerned, we obtain

$$\begin{aligned} g'(z) &= \frac{1 \times \exp(z) - (1+z)\exp(z)}{\exp(z)^2} \\ &= \frac{\exp(z)(1-1-z)}{\exp(z)^2} \\ &= \frac{-z}{\exp(z)}. \end{aligned}$$

The derivative of $g$ is obviously less than zero for all $z$ greater than zero. Hence, $g$ is a monotonically decreasing function and constantly less than one within the interval $(0, \infty)$. Hence, condition (45) holds.
Now we return to further analysis of function $f$. We have already shown that it is monotonically increasing for $z > 0$. But we still have to uncover on what conditions $f$ intersects the $x$-axes. For that reason, the limiting cases $z \to 0$ and $z \to \infty$ are considered:

$$\begin{aligned} \lim_{z\to 0} f(z) &= \lim_{z\to 0} \left[ \frac{z}{\theta\left(1 - \exp\left(-z\right)\right)} + z - r \right] \\ &= \lim_{z\to 0} \frac{1}{\theta \exp(-z)} + \lim_{z\to 0} z - r \\ &= \frac{1}{\theta} - r \end{aligned} \tag{47}$$

$$\begin{aligned} \lim_{z\to\infty} f(z) &= \lim_{z\to\infty} \left[ \frac{z}{\theta\left(1 - \exp\left(-z\right)\right)} + z - r \right] \\ &= \infty \end{aligned} \tag{48}$$

By now, we know that $f$ is monotonically increasing and converging to infinity for increasing $z$. So, it only depends on (47) if $f$ intersects the abscissa or not. If $\frac{1}{\theta}$ is greater than $r$, function $f$ is positive for all values of $z$ greater than zero (see Fig. 30). If $\frac{1}{\theta}$ is less than $r$, function $f$ is negative for values of

$z$ near zero. For growing $z$ function $f$ finally becomes positive and converges to infinity (see Fig. 31).[82]

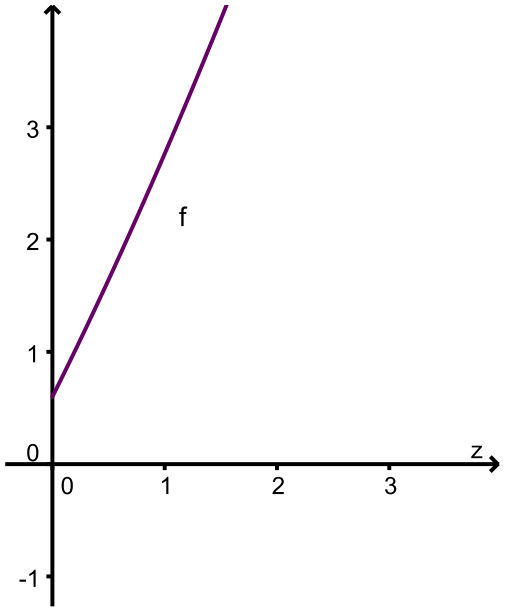



Fig. 30: Here the parameters are given by $r = 1.4$ and $\theta = 0.5$. In particular, the term $\frac{1}{\theta}$ is greater than $r$.

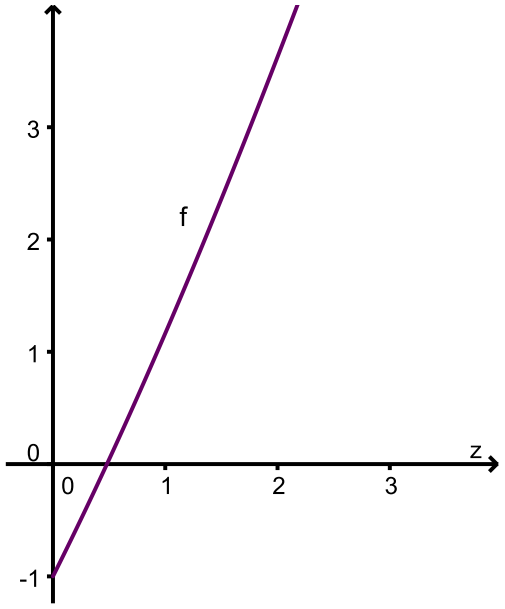



Fig. 31: Here the parameters are given by $r = 3$ and $\theta = 0.5$. In particular, the term $\frac{1}{\theta}$ is less than $r$.

Hence, in case of $\frac{1}{\theta} < r$, there is exactly one intersection point with the $x$-axes. Therefore, the isoclines of system (33), (34) intersect in exactly one point (see Fig. 33) since, by definition of $f$,

$$f(z) = \frac{z}{\theta\left(1 - \exp\left(-z\right)\right)} - (r - z),$$

this intersection point is the unique, positive solution to

$$x_t = \begin{cases} r - y_t \\ \frac{y_t}{\theta(1-\exp(-y_t))}. \end{cases}$$

Otherwise, i. e. if $f$ does not intersect the abscissa, only the equilibria on the boundary exist (see Fig. 32).[83]

[82] Kon & Takeuchi 2001b, p. 289
[83] Kon & Takeuchi 2001b, p. 289

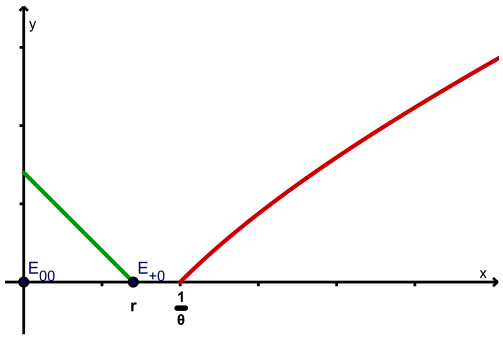



Fig. 32: Here the parameters are given by $r = 1.4$ and $\theta = 0.5$. The $x$-isocline (green) and the $y$-isocline (red) do not intersect.

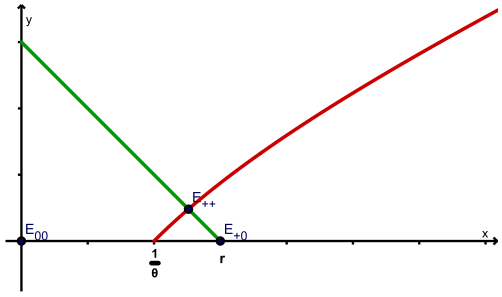



Fig. 33: Here the parameters are given by $r = 3$ and $\theta = 0.5$. The $x$-isocline (green) and the $y$-isocline (red) intersect.

The following part of this section is devoted to the stability analysis of the three equilibria $E_{00}$, $E_{+0}$ and $E_{++}$. Using the Jury criterion will reveal the stability properties of these fixed points.[84]
We start the investigations by linearizing system (33), (34)

$$f_1 := x_{t+1} = x_t \exp(r - x_t - y_t)$$

$$f_2 := y_{t+1} = \theta x_t \left(1 - \exp(-y_t)\right).$$

For that reason, we differentiate $f_1$ and $f_2$ with respect to $x_t$ and $y_t$,

$$\begin{aligned}
\frac{\delta f_1}{\delta x_t} &= \exp(r - x_t - y_t) + x_t \exp(r - x_t - y_t)(-1) \\
&= \exp(r - x_t - y_t)(1 - x_t) \\
\frac{\delta f_1}{\delta y_t} &= x_t \exp(r - x_t - y_t)(-1) \\
&= -x_t \exp(r - x_t - y_t) \\
\frac{\delta f_2}{\delta x_t} &= \theta \left(1 - \exp(-y_t)\right) \\
\frac{\delta f_2}{\delta y_t} &= -\theta x_t \exp(-y_t)(-1) \\
&= \theta x_t \exp(-y_t).
\end{aligned}$$

[84] See section 2.

These partial derivatives are now summed up in the Jacobian matrix $J(x_t, y_t)$.

$$J(x_t, y_t) = \begin{pmatrix} \exp(r - x_t - y_t)(1 - x_t) & -x_t \exp(r - x_t - y_t) \\ \theta\,(1 - \exp(-y_t)) & \theta x_t \exp(-y_t) \end{pmatrix}. \tag{49}$$

One after another, the three equilibria of system (33), (34) will be plugged in into the Jacobian (49). We start with $E_{00} = (0, 0)$,

$$\begin{aligned} J(E_{00}) &= \begin{pmatrix} \exp(r) & 0 \\ 0 & 0 \end{pmatrix} \\ &= \exp(r). \end{aligned}$$

The fixed point $E_{00}$ is stable if and only if $\exp(r) < 1$. This inequality only holds for $r < 0$. Since we assumed that $r$ is always greater than zero, this inequality is never fulfilled. Hence, $E_{00}$ is always unstable.[85]
Considering now $E_{+0} = (r, 0)$ the Jacobian matrix (49) transforms to

$$\begin{aligned} J(E_{+0}) &= \begin{pmatrix} \exp(0)(1 - r) & -r \exp(0) \\ 0 & \theta r \exp(0) \end{pmatrix} \\ &= \begin{pmatrix} 1 - r & -r \\ 0 & \theta r \end{pmatrix}. \end{aligned}$$

The matrix $J(E_{+0})$ is a triangular matrix. Hence, the eigenvalues are given by the entries of the main diagonal. If the spectral radius, that is the maximum of the absolute values of the eigenvalues, is less than one, then $E_{+0}$ is asymptotically stable. Therefore, take a closer look at the eigenvalues $\lambda_1 = 1 - r$ and $\lambda_2 = \theta r$.
The eigenvalue $\lambda_2$ is always greater than zero since the parameters $\theta$ and $r$ are assumed to be greater than zero. Hence,

$$|\lambda_2| < 1 \Leftrightarrow \theta r < 1 \tag{50}$$

and

$$|\lambda_1| < 1 \Leftrightarrow \begin{cases} 1 - r < 1 \Leftrightarrow r > 0 \\ -1 + r < 1 \Leftrightarrow r < 2 \end{cases} \Leftrightarrow 0 < r < 2. \tag{51}$$

[85] Kon 2006, p. 174

Equation (50) and (51) imply that $E_{+0}$ is asymptotically stable if and only if $\theta r < 1$ and $r < 2$. In case of $r < 2$ and $\theta r > 1$ fixed point $E_{+0}$ becomes a saddle. Its stable manifold is the $x$-axes. For $\theta r > 1$ the inner fixed point $E_{++}$ appears as it is shown in Fig. 35.[86]
The dynamics of system (33), (34) dependent of $\theta r$ are illustrated in the figures below:

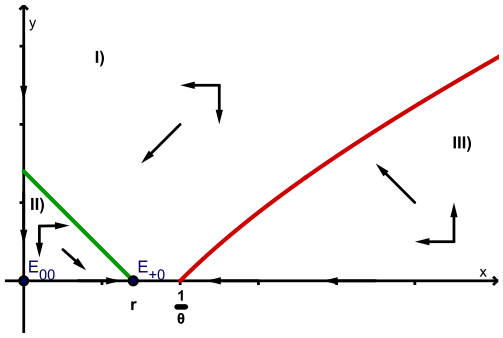



Fig. 34: Here the parameters are given by $r = 1.4$ and $\theta = 0.5$.

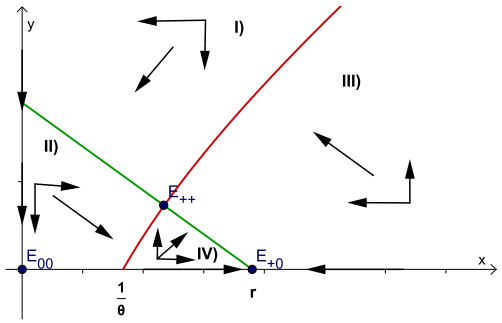



Fig. 35: Here the parameters are given by $r = 1.9$ and $\theta = 1.2$.

Fig. 34 illustrates the case where the dynamics of system (33), (34) converge to the fixed point $E_{+0}$ at the boundary for any positive initial condition.[87] Hence, since $y_t \to 0$ for $t \to \infty$, we get that

$$\lim_{t\to\infty} P_t = \lim_{t\to\infty} \frac{1}{b} y_t = \frac{1}{b} \lim_{t\to\infty} y_t = 0.$$

Therefore, whenever $\theta r < 1$ and $r < 2$, the parasitoid species will die out while the density of the host population converges to the positive equilibrium $r$.
As mentioned before, in the case of $r < 2$ and $\theta r > 1$ the boundary fixed point $E_{+0}$ is a saddle with the $x$-axes as stable manifold (see Fig. 35).
In both cases, every trajectory starting at the $y$-axes is mapped to the origin $(0, 0)$ by one iteration. It is easy to see that both axes are forward invariant, this means that if an orbit starts on the $x$- or the $y$-axes, it will stay at the $x$- and the $y$-axes, respectively. A trajectory starting on the $x$-axes will always

[86] Kon 2006, pp. 174 f.
[87] Kon 2006, p. 174

converge to $E_{+0}$ if $r$ is less than two except for the case where the initial condition is given by $x_0 = 0$. In this case, $x_t$ will stay at zero for all time.[88] The explicit calculations providing the dynamics (illustrated by the black arrows in Fig. 34 and in Fig. 35) of the rescaled system (33), (34) are obtained by solving following inequalities,

$$\begin{aligned}
x_{t+1} - x_t < 0 &\Leftrightarrow x_t \exp(r - x_t - y_t) - x_t < 0 \\
&\Leftrightarrow x_t \left(\exp(r - x_t - y_t) - 1\right) < 0 \\
&\Leftrightarrow \exp(r - x_t - y_t) - 1 < 0 \\
&\Leftrightarrow \exp(r - x_t - y_t) < 1 \\
&\Leftrightarrow r - x_t - y_t < 0 \\
&\Leftrightarrow r - x_t - y_t < 0 \\
&\Leftrightarrow x_t > r - y_t
\end{aligned}$$

$$\begin{aligned}
y_{t+1} - y_t < 0 &\Leftrightarrow \theta x_t \left(1 - \exp(-y_t)\right) - y_t < 0 \\
&\Leftrightarrow \theta x_t \left(1 - \exp(-y_t)\right) < y_t \\
&\Leftrightarrow x_t < \tfrac{y_t}{\theta(1 - \exp(-y_t))}.
\end{aligned}$$

According to the preceding calculations the dynamics in area I), II), III) and IV) are:

| Quadrant | Dynamic | Biological Consequence |
|---|---|---|
| I) | $x_{t+1} - x_t < 0$ and $y_{t+1} - y_t < 0$ $\swarrow$ | The host and the parasitoid population are decreasing. |
| II) | $x_{t+1} - x_t > 0$ and $y_{t+1} - y_t < 0$ $\searrow$ | The host pop. increases while the parasitoid pop. decreases. |
| III) | $x_{t+1} - x_t < 0$ and $y_{t+1} - y_t > 0$ $\nwarrow$ | The host pop. decreases while the parasitoid pop. increases. |
| IV) | $x_{t+1} - x_t > 0$ and $y_{t+1} - y_t > 0$ $\nearrow$ | The host and the parasitoid population are increasing. |

The obtained results concerning existence and stability of $E_{00}$, $E_{+0}$ and $E_{++}$

[88] Kon 2006, p. 175

are illustrated in following graphic.[89]

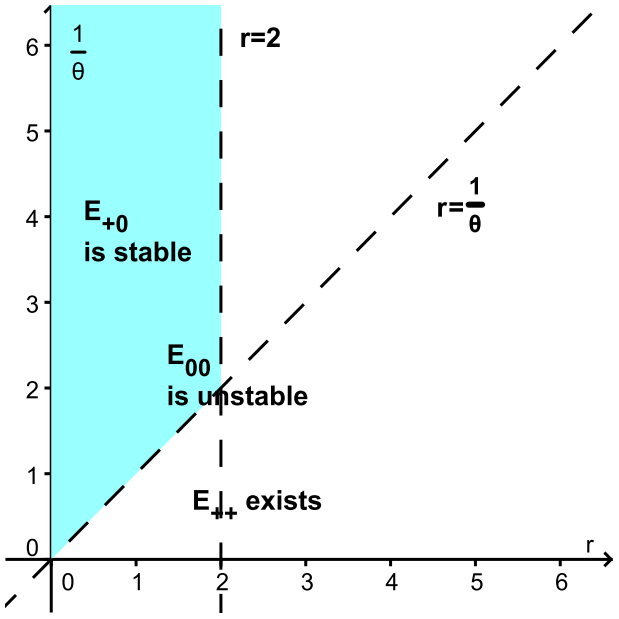



Fig. 36: The parameters $r$ and $\theta$ determine the existence and stability of the 3 fixed points.

It remains to investigate the stability of the inner fixed point $E_{++}$. Again we plug the fixed point in into the Jacobian matrix (49). We will use (40),

$$r = x^* + y^*,$$

to substitute $y^*$ by

$$y^* = r - x^*.$$

[89]For further illustration of the stability properties of $E_{+0}$ and $E_{++}$ see Kon 2006, p. 175.

This yields

$$\begin{aligned} J(E_{++}) &= \begin{pmatrix} \exp(r-x^*-y^*)(1-x^*) & -x^*\exp(r-x^*-y^*) \\ \theta\,(1-\exp(-y^*)) & \theta x^*\exp(-y^*) \end{pmatrix} \\ &= \begin{pmatrix} \exp(r-x^*-(r-x^*))(1-x^*) & -x^*\exp(r-x^*-(r-x^*)) \\ \theta\left(1-\left(-\frac{y^*}{x^*\theta}+1\right)\right) & \theta x^*\left(-\frac{y^*}{x^*\theta}+1\right) \end{pmatrix} \\ &= \begin{pmatrix} 1-x^* & -x^* \\ \frac{y^*}{x^*} & -y^*+\theta x^* \end{pmatrix} \qquad (52) \\ &= \begin{pmatrix} 1-x^* & -x^* \\ \frac{r-x^*}{x^*} & -r+x^*(1+\theta) \end{pmatrix}. \end{aligned}$$

The entries of the Jacobian (49) have reduced to rather simple expressions. The term $\exp(-y^*)$ has been replaced by $-\frac{y^*}{x^*\theta}+1$ in (52). This expression is obtained by transforming (41),

$$\begin{aligned} & x^* &=& \frac{y^*}{\theta(1-\exp(-y^*))} \\ \Leftrightarrow\quad & \frac{x^*}{y^*}\theta &=& \frac{1}{1-\exp(-y^*)} \\ \Leftrightarrow\quad & \frac{y^*}{x^*\theta} &=& 1-\exp(-y^*) \\ \Leftrightarrow\quad & -\frac{y^*}{x^*\theta}+1 &=& \exp(-y^*). \end{aligned}$$

Since we want to apply the Jury criterion, we consider the determinant and the trace of $J(E_{++})$.[90] Hence,

$$\begin{aligned} \det(J(E_{++})) &= (1-x^*)(x^*(1+\theta)-r)+r-x^* \\ &= x^*(1+\theta)-r-(x^*)^2(1+\theta)+rx^*+r-x^* \\ &= (1+\theta+r-1)x^*-(1+\theta)(x^*)^2 \\ &= (\theta+r)x^*-(1+\theta)(x^*)^2 \end{aligned}$$

$$\begin{aligned} \operatorname{tr}(J(E_{++})) &= 1-x^*+x^*(1+\theta)-r \\ &= 1-x^*+x^*+\theta x^*-r \\ &= 1+\theta x^*-r. \end{aligned}$$

In order to show that the inner fixed point $E_{++}$ is stable provided that $\theta r > 1$, we have to verify the Jury criterion

$$\det(J(E_{++})) \;<\; 1 \qquad (53)$$

[90] Kon & Takeuchi 2001b, p. 299

$$1 + \mathrm{tr}(J(E_{++})) + \det(J(E_{++})) \;>\; 0 \tag{54}$$

$$1 - \mathrm{tr}(J(E_{++})) + \det(J(E_{++})) \;>\; 0. \tag{55}$$

Condition (55) holds true whenever $\theta r > 1$, i. e. whenever $E_{++}$ exists.[91] This assertion will be shown by using the help function[92]

$$h(z) := 1 - 2z\exp(-z) - \exp(-z)^2. \tag{56}$$

The function $h(z)$ is positive for $z > 0$ since it fulfills

1.
$$h(0) = 0 \tag{57}$$

and

2.
$$h'(z) > 0 \text{ for } z > 0. \tag{58}$$

Properties (57) and (58) can by verified easily by plugging in 0 into $h(z)$,

$$h(0) = 1 - 0 \times \exp(0) - \exp(0)^2 = 0,$$

and by computing the derivative of $h(z)$,

$$\begin{aligned} h'(z) = \frac{dh(z)}{dz} &= -2z\exp(-z)(-1) - 2\exp(-z) - 2\exp(-z)\exp(-z)(-1) \\ &= 2\exp(-z)\underbrace{(-1 + z + \exp(-z))}_{=:h_1(z)}. \end{aligned}$$

Hence, we get that $h(0) = 0$ and that $h$ is monotonically increasing for $z > 0$ since $2\exp(-z)$ is obviously positive and $h_1(z)$ fulfills

1.
$$h_1(0) = -1 + 0 + 1 = 0$$

and

[91] Kon & Takeuchi 2001b, p. 299
[92] Kon & Takeuchi 2001b, p. 299

2.

$$h_1'(z) = 1 - \exp(-z) > 0 \text{ for } z > 0.$$

Thus, function $h$ is positive for all $z > 0$, just see

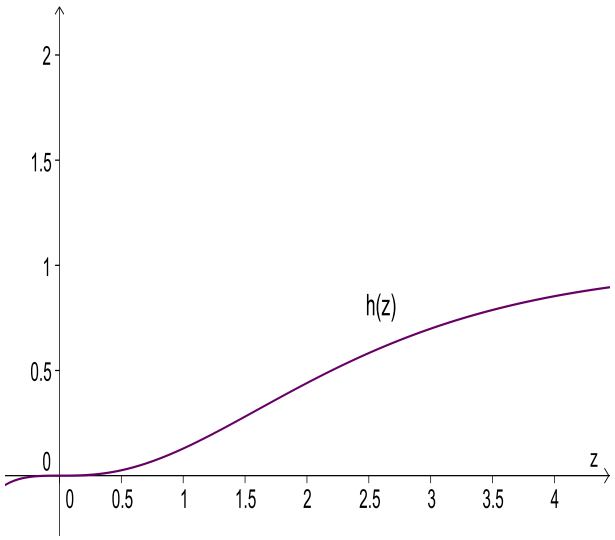



Fig. 37: This figure shows $h(z)$.

With the help of the preceding result, one can show that the following inequality holds for $z > 0$:

$$\frac{z}{1 - \exp(-z)} > \frac{1}{2}(z + 2) \tag{59}$$

In order to prove inequality (59) to be true, define[93]

$$g(z) := \frac{z}{1 - \exp(-z)} - \frac{1}{2}(z + 2) \tag{60}$$

and check the following properties of $g$,

1.

$$\lim_{z \to 0} g(z) = 0 \tag{61}$$

and

[93]Kon & Takeuchi 2001b, p. 299

2.

$$g'(z) > 0 \text{ for } z > 0. \tag{62}$$

Condition (61) and (62) can be verified easily since

$$\begin{aligned} \lim_{z\to 0} g(z) &= \lim_{z\to 0} \left[ \tfrac{z}{1-\exp(-z)} - \tfrac{1}{2}(z+2) \right] \\ &= \lim_{z\to 0} \tfrac{1}{\exp(-z)} - \lim_{z\to 0} \tfrac{1}{2}(z+2) \\ &= \tfrac{1}{1} - 1 \\ &= 0 \end{aligned}$$

and

$$\begin{aligned} g'(z) = \frac{dg(z)}{dz} &= \frac{1-\exp(-z) - z(-\exp(-z)(-1))}{(1-\exp(-z))^2} - \frac{1}{2} \\ &= \frac{2 - 2\exp(-z) - 2z\exp(-z) - (1-\exp(-z))^2}{2(1-\exp(-z))^2} \\ &= \frac{2 - 2\exp(-z) - 2z\exp(-z) - 1 + 2\exp(-z) - \exp(-z)^2}{2(1-\exp(-z))^2} \\ &= \frac{1}{2(1-\exp(-z))^2} \underbrace{\left(1 - 2z\exp(-z) - \exp(-z)^2\right)}_{=h(z)}. \end{aligned} \tag{63}$$

Since the factor $\frac{1}{2(1-\exp(-z))^2}$ in (63) is obviously greater than zero for all positive $z$ and $h(z)$ is greater than zero as well for $z > 0$, the derivative of $g$ is positive for all positive values of $z$. Hence, property (62) holds, $g$ is positive for $z > 0$ and thus, inequality (59) is fulfilled.[94]
The next figure illustrates the properties of function $g$.

[94]Kon & Takeuchi 2001b, p. 299

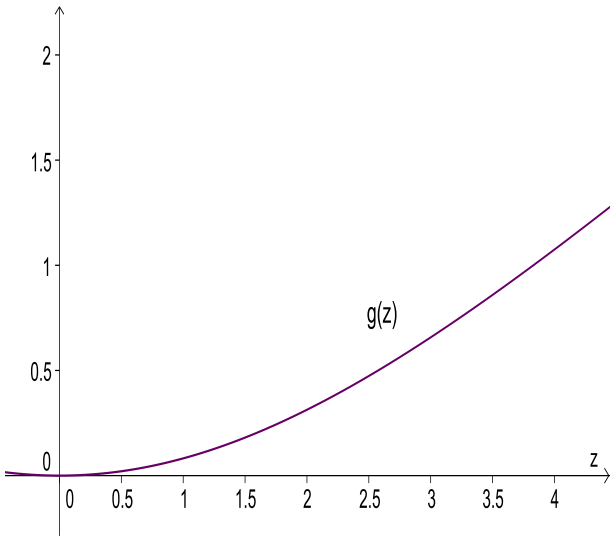



Fig. 38: This figure shows $g(z)$.

Inequality (59) implies

$$\frac{y^*}{1-\exp(-y^*)} > \frac{1}{2}(y^*+2). \tag{64}$$

From (64) and the form of isocline (41) follows

$$\theta x^* > \frac{1}{2}(y^*+2). \tag{65}$$

By replacing $y^*$ by $y^* = r - x^*$ in (65), we obtain

$$\theta x^* > \frac{1}{2}(r-x^*+2). \tag{66}$$

Now transform (66), this yields

$$\begin{array}{rcl} \theta x^* + \frac{x^*}{2} & > & \frac{r+2}{2} \\ \Leftrightarrow \quad x^*\left(\theta+\frac{1}{2}\right) & > & \frac{r+2}{2} \\ \Leftrightarrow \quad x^* & > & \frac{r+2}{2\left(\theta+\frac{1}{2}\right)}, \end{array}$$

which is equivalent to[95]

$$x^* > \frac{r+2}{(2\theta+1)}. \tag{67}$$

[95]Kon & Takeuchi 2001b, p. 300

We will now derive further inequalities like (67) in order to prove condition (55).

Therefore, define[96]

$$k(z) := 1 + z - \frac{z}{1 - \exp(-z)} \tag{68}$$

in order to show

$$1 + z > \frac{z}{1 - \exp(-z)} \tag{69}$$

for $z > 0$.

First, check following properties of $k$,

1.
$$\lim_{z \to 0} k(0) = 0 \tag{70}$$

and

2.
$$k(z) > 0 \text{ for } z > 0. \tag{71}$$

Again, properties (70) and (71) can be verified easily since

$$\begin{aligned} \lim_{z \to 0} k(z) &= 1 + \lim_{z \to 0} z - \lim_{z \to 0} \frac{1}{\exp(-z)} \\ &= 1 + 0 - 1 \\ &= 0 \end{aligned}$$

and

$$\begin{aligned} k'(z) = \frac{dk(z)}{dz} &= 1 - \frac{1 - \exp(-z) - z\exp(-z)}{(1 - \exp(-z))^2} \\ &= \frac{(1 - \exp(-z))^2 - 1 + \exp(-z) + z\exp(-z)}{(1 - \exp(-z))^2} \\ &= \frac{1 - 2\exp(-z) + \exp(-z)^2 - 1 + \exp(-z) + z\exp(-z)}{(1 - \exp(-z))^2} \\ &= \frac{\exp(-z)}{(1 - \exp(-z))^2} \underbrace{(-1 + z + \exp(-z))}_{:= k_1(z)}. \end{aligned} \tag{72}$$

The derivative of $k$ is greater than zero for all $z > 0$ since $\frac{\exp(-z)}{(1-\exp(-z))^2}$ and the factor $k_1(z)$ are both positive for $z > 0$. In particular, function $k_1(z)$ fulfills

[96] Kon & Takeuchi 2001b, p. 300

1.

$$k_1(0) = -1 + 0 + 1 = 0$$

and

2.

$$k_1'(z) = 1 - \exp(-z) > 0 \text{ for } z > 0.$$

Hence, $k$ is a positive function for $z > 0$ and so (69) holds. For illustration just see

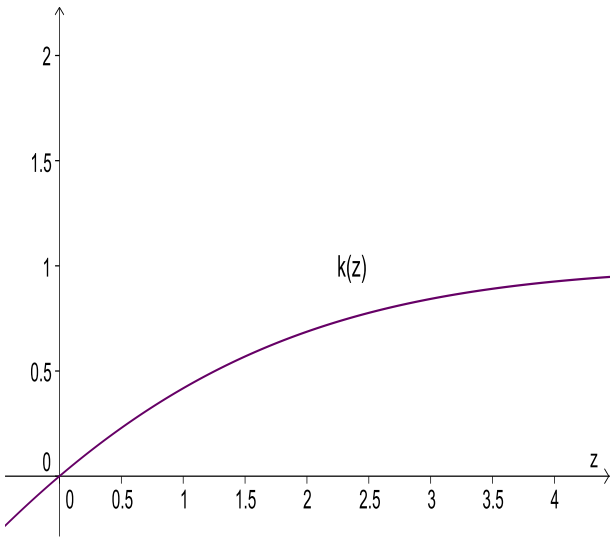



Fig. 39: This figure shows $k(z)$.

With the help of inequality (69), one can obtain the following estimate for $x^*$,

$$\theta x^* = \frac{y^*}{1 - \exp(-y^*)} \quad < \quad y^* + 1. \tag{73}$$

Inequality (73) is transformed, which results in

$$\begin{array}{rcl} \theta x^* & < & y^* + 1 \\ \Leftrightarrow \quad r - x^* + 1 & > & \theta x^* \\ \Leftrightarrow \quad r + 1 & > & x^*(\theta + 1). \end{array}$$

These computations imply[97]

$$x^* \quad < \quad \frac{r+1}{\theta+1}. \tag{74}$$

We have already managed to obtain

$$\tfrac{r+2}{(2\theta+1)} \quad < \quad x^* \quad < \quad \tfrac{r+1}{\theta+1}$$

with the help of (67) and (74). Next, introduce function[98]

$$q(z) := r + rz - (\theta+1)z^2. \tag{75}$$

Function $q(z)$ has a global maximum at $z_{max} = \frac{r}{2(\theta+1)}$ since

$$\begin{array}{rcccl} q'(z) & = & r - 2(\theta+1)z & = & 0 \\ & \Leftrightarrow & 2(\theta+1)z & = & r \\ & \Leftrightarrow & z = \frac{r}{2(\theta+1)}. & & \end{array}$$

Since it is obvious that

$$r < r+2$$

and

$$2(\theta+1) > 2\theta+1$$

the following relation holds,

$$\frac{r}{2(\theta+1)} \quad < \quad \frac{r+2}{2\theta+1}. \tag{76}$$

Now using (67), (74) and (76) yields

$$\tfrac{r}{2(\theta+1)} \quad < \quad \underbrace{\frac{r+2}{(2\theta+1)}}_{=:s_1} \quad < \quad x^* \quad < \quad \underbrace{\frac{r+1}{\theta+1}}_{=:s_2}. \tag{77}$$

This result is illustrated in the graphic below showing (77) in addition to function $q(z)$,

[97] Kon & Takeuchi 2001b, p. 300
[98] Kon & Takeuchi 2001b, p. 300

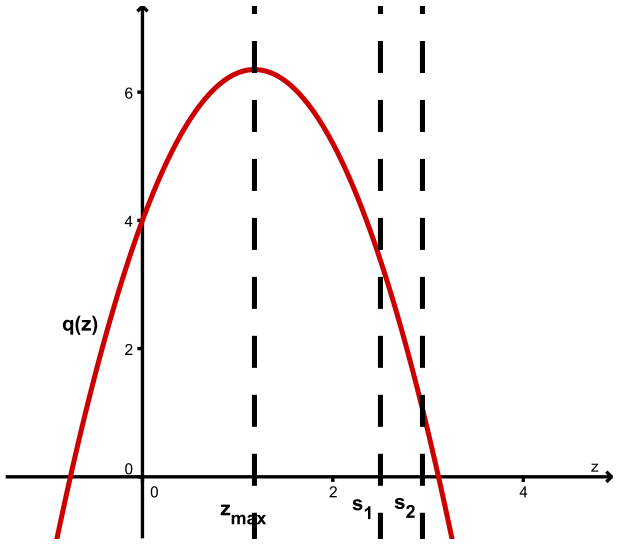



Fig. 40: The parameters are given by $r = 4$ and $\theta = 0.7$.

where $z_{max} = \frac{r}{2(\theta+1)}$. Since (77) holds and $z_{max} = \frac{r}{2(\theta+1)}$ is the value of the global maximum of $q$, we know that[99]

$$q(x^*) \quad > \quad q(s_2) = q\left(\frac{r+1}{\theta+1}\right). \tag{78}$$

If one plugs in $s_2$ into $q(z)$, one obtains

$$\begin{aligned} q\left(\frac{r+1}{\theta+1}\right) &= r + r\frac{r+1}{\theta+1} - (\theta+1)\left(\frac{r+1}{\theta+1}\right)^2 \\ &= \frac{r(\theta+1) + r(r+1) - (r+1)^2}{\theta+1} \\ &= \frac{1}{\theta+1}(r + r\theta + r^2 + r - r^2 - 2r - 1) \\ &= \frac{1}{\theta+1}(r\theta - 1). \end{aligned} \tag{79}$$

The right hand side of equation (79) is positive for $\theta r > 1$. Since

$$q(x^*) = r + rx^* - (\theta+1)(x^*)^2$$

just gives (55) and since (78) holds, we get that

$$r + rx^* - (\theta+1)(x^*)^2 > \frac{1}{\theta+1}(r\theta - 1) > 0$$

[99] Kon & Takeuchi 2001b, p. 300

for $\theta r > 1$. Thus, equality (55) holds if the positive equilibrium $E_{++}$ exists.[100] Now we want to focus on the equilibrium $E_{+0} = (r, 0)$ on the $x$-axes. The dynamics on the $y$-axes have already been investigated above. These investigations have shown that $E_{00}$ is the only fixed point on the $y$-axes.
If we look at the dynamics on the $x$-axes,[101] equation (33),

$$x_{t+1} = x_t \exp(r - x_t - y_t),$$

reduces to

$$x_{t+1} = x_t \exp(r - x_t). \tag{80}$$

Equality (80) is called the Ricker map. It will be treated in more detail in section 8.2. We have already seen that the equilibrium $E_{+0}$ is stable for $r < 2$. In section 8.2 the analysis of the Ricker map (80) for $r$ growing beyond the value 2 will be given. At the moment we rather want to obtain the conditions for stability of an arbitrary m-cycle on the $x$-axis. Hence, again we use the Jacobian matrix (49) of system (33), (34) and plug in the m-cycle $\{(p_t, 0)\}_{t=1}^m$ into

$$\prod_{t=1}^{m} J(p_t, 0).$$

This yields

$$\begin{aligned} \prod_{t=1}^{m} J(p_t, 0) &= \prod_{t=1}^{m} \begin{pmatrix} \exp(r - p_t)(1 - p_t) & -p_t \exp(r - p_t) \\ \theta\,(1 - \exp(0)) & \theta p_t \exp(0) \end{pmatrix} \\ &= \prod_{t=1}^{m} \begin{pmatrix} \exp(r - p_t)(1 - p_t) & -p_t \exp(r - p_t) \\ 0 & \theta p_t \end{pmatrix}. \end{aligned}$$

The eigenvalues of this triangular matrix can be found in the main diagonal.[102] They are

$$\prod_{t=1}^{m} \exp(r - p_t)(1 - p_t) \tag{81}$$

and

$$\prod_{t=1}^{m} \theta p_t. \tag{82}$$

[100] Kon & Takeuchi 2001b, p. 300
[101] Kon 2006, pp. 175-177
[102] Kon & Takeuchi 2001a, pp. 1390 f.

The m-cycle $\{(p_t, 0)\}_{t=1}^m$ is stable if the spectral radius $\rho(\prod_{t=1}^m J(p_t, 0))$ is less than 1. Hence, we have to check if

$$\left|\prod_{t=1}^m \exp(r - p_t)(1 - p_t)\right| < 1 \tag{83}$$

and

$$\prod_{t=1}^m \theta p_t < 1 \tag{84}$$

hold.

The first condition, (83) is the so-called internal stability since it represents the condition for stability of an m-cycle of the Ricker map (80).[103] The investigation of inequality (83) is therefore left to section 8.2. We will reveal that for growing $r$ there will appear orbits of increasing number in periods.

The second condition, (84) is called transversal stability. We have a saturated m-cycle $\{(p_t, 0)\}_{t=1}^m$ if $\prod_{t=1}^m \theta p_t \leq 1$, otherwise the m-cycle is said to be unsaturated.[104]

As has already been illustrated in Fig. 34, the fixed point $E_{+0} = (r, 0)$ is globally asymptotically stable for $r < 2$ and $\theta r < 1$. In particular, the equilibrium is strictly saturated under the condition $\theta r < 1$. We will now show that every cycle on the boundary is saturated if the equilibrium $E_{+0}$ is.

We start by proving that the time average of each cycle $\{p_t\}_{t=1}^m$ equals the positive equilibrium $r$ on the $x$-axes. Hence, we have to show that

$$\frac{1}{m}\sum_{t=1}^m p_t = r \tag{85}$$

for every cycle $\{p_t\}_{t=1}^m$.

We start by transforming the Ricker map (80),

$$x_{t+1} = x_t \exp(r - x_t),$$

to

$$\frac{x_{t+1}}{x_t} = \exp(r - x_t). \tag{86}$$

[103] Kon 2006, p. 176

[104] Kon 2006, p. 176

Now replace $x_t$ by the periodic point $p_t$ in (86), apply the logarithm on both sides and sum up from $t = 1$ to $t = m$, i. e. over 1 period. This yields

$$\sum_{t=1}^{m} \log(p_{t+1}) - \log(p_t) \;\; = \;\; \sum_{t=1}^{m} r - \sum_{t=1}^{m} p_t. \tag{87}$$

Now write the sum on the left-hand of (87) out in full. Most terms short out,

$$\log(p_{m+1}) - \log(p_m) + \log(p_m) - \log(p_{m-1}) + \cdots + \log(p_2) - \log(p_1) = mr - \sum_{t=1}^{m} p_t.$$

Since the cycle $\{p_t\}_{t=1}^{m}$ is of period $m$, we have that $p_{m+1} = p_1$. Hence, (87) turns to

$$0 = mr - \sum_{t=1}^{m} p_t$$

which is equivalent to

$$\frac{1}{m} \sum_{t=1}^{m} p_t = r.$$

With the help of (85) and the fact that the geometric mean is equal or less to the arithmetic mean,

$$\left( \prod_{i=1}^{n} z_i \right)^{\frac{1}{n}} \leq \sum_{i=1}^{n} \frac{z_i}{n}, \tag{88}$$

we can confirm the assertion that if the fixed point $E_{+0}$ is strictly saturated, then all other cycles are strictly saturated as well.[105] Apply result (88) and (85) on the second eigenvalue (82) of $\prod_{t=1}^{m} J(p_t, 0)$, namely on $\prod_{t=1}^{m} \theta p_t$. We obtain

$$\left( \prod_{t=1}^{m} \theta p_t \right)^{\frac{1}{m}} \leq \frac{1}{m} \sum_{t=1}^{m} \theta p_t = \theta r. \tag{89}$$

Hence, if $E_{+0}$ is strictly saturated, i. e. if $\theta r < 1$, then following relation holds for (89),

$$\left( \prod_{t=1}^{m} \theta p_t \right)^{\frac{1}{m}} < 1. \tag{90}$$

[105] Kon 2006, p. 177

Inequality (90) finally implies

$$\prod_{t=1}^{m} \theta p_t < 1 \text{ whenever } \theta r < 1.$$

Therefore, if $E_{+0} = (r, 0)$ is transversally stable, all cycles are as well.[106]

[106] Kon 2006, pp. 176 f.

# 6 Detailed Analysis of the Nicholson-Bailey Model

Let $H$ and $H'$ denote the host density of the present generation and the host density of the following generation, respectively. Analogously, $P$ and $P'$ represent the density of the present and upcoming parasitoid generation, respectively.

## 6.1 The Original Nicholson-Bailey Model

This subsection is devoted to a more detailed analysis of the original Nicholson-Bailey model[107]

$$H' = \lambda H g(P) \tag{91}$$

$$P' = \omega H (1 - g(P)) \tag{92}$$

where $g(x) = \exp(-bx)$.
It will be shown that the original Nicholson-Bailey model has a positive fixed point but that it is not stable.

### 6.1.1 Computation of the Isoclines and Fixed Point(s)

The $H$-isocline is given by:

$$\begin{array}{rcccccccc} & H & = & \lambda H \exp(-bP) & & & & & \\ \Leftrightarrow & H & = & 0 & \text{or} & 1 & = & \lambda \exp(-bP) \\ & & & & \Leftrightarrow & \exp(bP) & = & \lambda \\ & & & & \Leftrightarrow & bP & = & \ln \lambda \\ & & & & \Leftrightarrow & P & = & \frac{\ln \lambda}{a} \end{array}$$

The $P$-isocline is given by:

$$\begin{array}{rcccccc} & P & = & \omega H (1 - \exp(-bP)) & & & \\ \Leftrightarrow & P & = & 0 & \text{or} & H & = & \frac{P}{\omega(1-\exp(-bP))} \end{array}$$

[107] Nicholson & Bailey 1935, p. 551-598

The point $(H_0^*, P_0^*) = (0, 0)$ is an equilibrium of the system (91), (92) for any given set of parameters. Under the condition that $\lambda > 1$ another fixed point, $(H^*, P^*)$, exists. It is obtained by intersecting the two isoclines,

$$\begin{aligned} H^* &= \frac{\frac{\ln\lambda}{b}}{\omega\left(1-e^{-b\frac{\ln\lambda}{b}}\right)} \\ \Leftrightarrow \quad H^* &= \frac{\ln\lambda}{\omega b\left(1-\frac{1}{\lambda}\right)}. \end{aligned}$$

The point $(H^*, P^*)$ is an inner equilibrium and is given by $(H^*, P^*) = \left(\frac{\lambda\ln\lambda}{(\lambda-1)b\omega}, \frac{\ln\lambda}{b}\right)$.[108] The subsequent figure shows the isoclines and fixed points of the original Nicholson-Bailey model.[109]

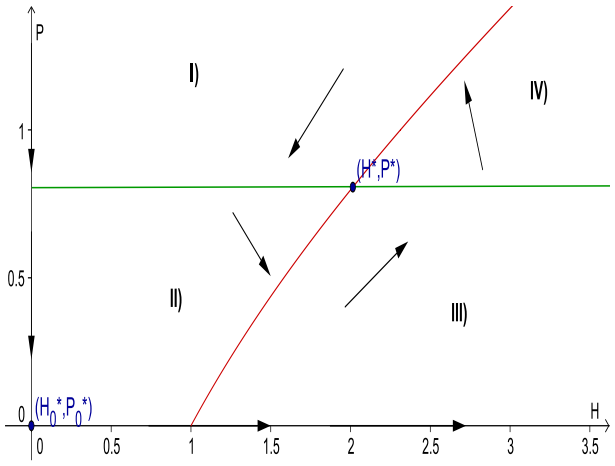



Fig. 41: This figure presents the $H-$ (green) and the $P$-isocline (red) for the parameters $b = 2$, $\lambda = 2$, $\omega = 0.5$. The inner fixed point $(H^*, P^*)$ is at $(2.01, 0.81)$.

A simple stability analysis of $(H_0^*, P_0^*)$ yields that for $\lambda < 1$ this equilibrium is asymptotically stable since we have

$$H' \leq \lambda H \Rightarrow H_t \to 0 \text{ as } t \to \infty$$

$$P' \leq \omega H \Rightarrow P_t \to 0 \text{ as } t \to \infty.$$

[108] Elaydi 1999, p. 211

[109] See section 6.2 for a detailed analysis of the dynamics represented by the vectors in Fig. 41.

Since this is true for any initial condition, $(H_0^*, P_0^*)$ is globally asymptotically stable. In the case of $\lambda > 1$, $(H_0^*, P_0^*)$ becomes unstable. This can be easily seen by the dynamics on the $x$-axes, they lead away from the origin. Formally, this means that in case of $P = 0$, the system reduces to

$$H' = \lambda H. \tag{93}$$

Equation (93) implies

$$H_t \to \infty \text{ as } t \to \infty.$$

In biological terms, equation (93) implies that the host populations will grow exponentially in the absence of parasitism.
For further stability analysis, system (91), (92) will be linearized by calculating the partial derivatives of

$$f_1 := H' = \lambda H \exp(-bP)$$

and

$$f_2 := P' = \omega H(1 - \exp(-bP))$$

with respect to $H$ and $P$:

$$\begin{aligned}
\tfrac{\delta f_1}{\delta H} &= \lambda \exp(-bP) \\
\tfrac{\delta f_1}{\delta P} &= -\lambda b H \exp(-bP) \\
\tfrac{\delta f_2}{\delta H} &= \omega(1 - \exp(-bP)) \\
\tfrac{\delta f_2}{\delta P} &= \omega b H \exp(-bP)
\end{aligned}$$

These results form the Jacobian-matrix $Df(x)$, where $f := \begin{pmatrix} f_1 \\ f_2 \end{pmatrix}$ and $x$ is some point in $\mathbb{R}^2$. Hence, the Jacobian matrix for (91), (92) has the following

form:

$$D(f(H,P)) = \begin{pmatrix} \lambda \exp(-bP) & -\lambda bH \exp(-bP) \\ \\ \omega(1-\exp(-bP)) & \omega bH \exp(-bP) \end{pmatrix}$$

Now the two fixed points will be plugged in into the matrix, beginning with $(H_0^*, P_0^*)$:

$$\begin{aligned} D(f(H_0^*, P_0^*)) &= \begin{pmatrix} \lambda & 0 \\ \\ 0 & 0 \end{pmatrix} \\ &= \lambda \end{aligned}$$

According to Theorem 2.2. the equilibrium $(H_0^*, P_0^*)$ is asymptotically stable for $\lambda < 1$ and unstable for $\lambda > 1$.
In the case of the inner fixed point $(H^*, P^*)$ the Jacobian matrix transforms to

$$\begin{aligned} D(f(H^*, P^*)) &= \begin{pmatrix} \lambda \exp(-\ln\lambda) & -\lambda bH^* \exp(-\ln\lambda) \\ \\ \omega(1-\exp(-\ln\lambda)) & \omega bH^* \exp(-\ln\lambda) \end{pmatrix} \\ &= \begin{pmatrix} 1 & -bH^* \\ \\ \omega(1-\frac{1}{\lambda}) & \frac{\omega bH^*}{\lambda} \end{pmatrix}. \end{aligned}$$

For further investigations concerning the stability of $(H^*, P^*)$ we will take a closer look at the trace and the determinant of $D(f(H^*, P^*))$,

$$\begin{aligned}
\operatorname{tr}(D(f(H^*,P^*))) &= 1+\tfrac{\omega b H^*}{\lambda} \\
\det(D(f(H^*,P^*))) &= \tfrac{\omega b H^*}{\lambda}+\omega b H^*(1-\tfrac{1}{\lambda}) \\
&= \omega b H^* \\
&= \tfrac{\lambda\ln\lambda}{\lambda-1}.
\end{aligned}$$

For arbitrary $\lambda > 0$ the determinant of $D(f(H^*, P^*))$ is obviously greater than zero. We will show that $\lambda > 1$ implies that the expression $\frac{\lambda \ln \lambda}{\lambda-1}$ is even greater than one.
Introduce

$$h(\lambda) := \lambda \ln \lambda - \lambda + 1$$

and differentiate it with respect to $\lambda$, then you get

$$\frac{dh}{d\lambda} = \ln\lambda + \lambda\frac{1}{\lambda} - 1 = \ln\lambda > 0$$

under the condition that $\lambda > 1$. Hence, since $h(\lambda)$ is increasing and $h(1) = 0$, we have that

$$h(\lambda) > 0 \text{ for all } \lambda > 1. \tag{94}$$

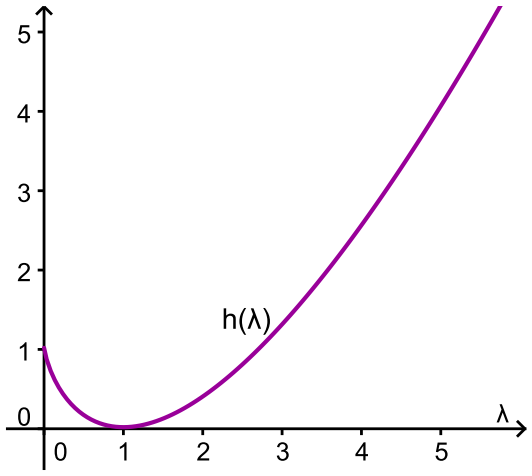



Fig. 42: This picture shows the function $h(\lambda)$.

Inequality (94) implies

$$\lambda \ln \lambda > \lambda - 1 \Leftrightarrow \frac{\lambda \ln \lambda}{\lambda - 1} > 1$$

for all $\lambda > 1$.

With the help of the preceding results the following relations are obtained:

$$\begin{aligned} 1 + \mathrm{tr}(D(f(H^*, P^*))) + \det(D(f(H^*, P^*))) &= 2 + \tfrac{\ln\lambda}{\lambda-1} + \tfrac{\lambda\ln\lambda}{\lambda-1} \\ &= 2 + \tfrac{\ln\lambda(\lambda+1)}{\lambda-1} \\ &> 0 \\ 1 - \mathrm{tr}(D(f(H^*, P^*))) + \det(D(f(H^*, P^*))) &= -\tfrac{\ln\lambda}{\lambda-1} + \tfrac{\lambda\ln\lambda}{\lambda-1} \\ &= \ln\lambda \\ &> 0 \\ \det(D(f(H^*, P^*))) &> 1 \end{aligned}$$

Since $\det(D(f(H^*, P^*))) > 1$, the Jury criterion[110] proves the inner equilibrium $(H^*, P^*)$ to be unstable. This result is illustrated by the picture below:

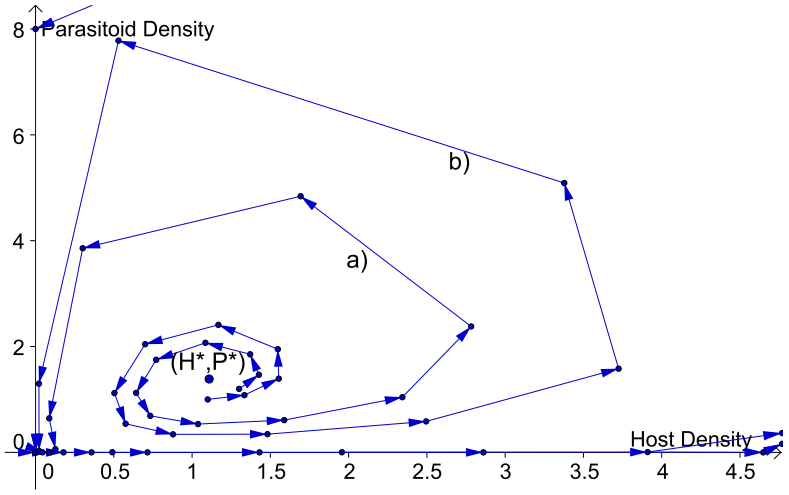



Fig. 43: The figure shows the phase plot of the original Nicholson-Bailey model for a given set of parameters, $b = 0.5$, $\lambda = 2$, $\omega = 2.5$. The inner fixed point $(H^*, P^*)$ of this system is at $(1.109, 1.386)$. The two solutions a) and b) start very close to the equilibrium with the initial conditions $(H_0, P_0) = (1.3, 1.2)$ for a) and $(H_0, P_0) = (1.1, 1)$ for b).

The stability analysis of system (91), (92) results in the following bifurcation diagrams for $H^*$ and for $P^*$, respectively. The stability properties (depending

[110] See section 2.

on $\lambda$) of $(H_0^*, P_0^*)$ and $(H^*, P^*)$ are visualized using continuous lines (fixed point is stable) and dashed lines (fixed point is unstable).

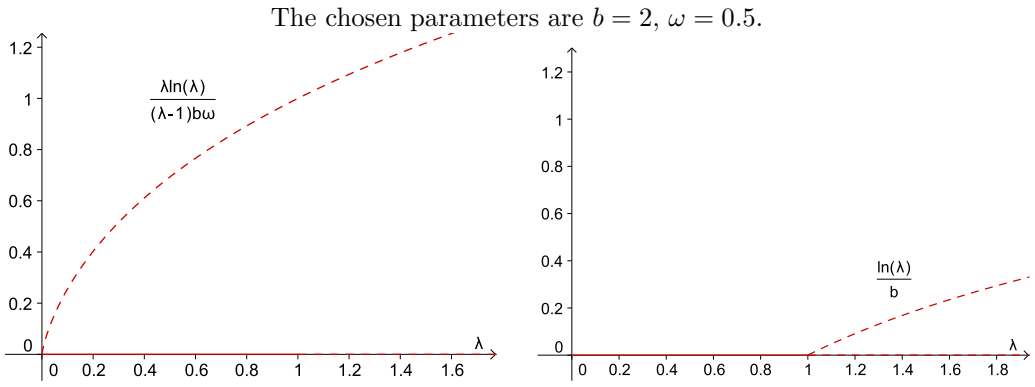



Fig. 44: The bifurcation diagrams show that $(H^*, P^*)$ is always unstable, whereas $(H_0^*, P_0^*)$ is stable for $\lambda < 1$.

## 6.2 The Nicholson-Bailey Model with Aggregated Search

This subsection will reveal that a sufficiently high level of aggregation of the parasitic attacks stabilizes the inner equilibrium. We will therefore look at the system[111]

$$H' = \lambda H g\left(P\right) \tag{95}$$

$$P' = \omega H\left(1 - g\left(P\right)\right) \tag{96}$$

where $g(x) = (1 + \frac{bx}{k})^{-k}$.

### 6.2.1 Computation of the Isoclines and Fixed Point(s)

The $H$-isocline is given by:

[111] May 1978, pp. 833-843

$$
\begin{array}{rcccccl}
 & H & = & \lambda H\left(1+\frac{bP}{k}\right)^{-k} & & & \\
\Leftrightarrow & H & = & 0 & \text{or} & 1 & = \lambda\left(1+\frac{bP}{k}\right)^{-k} \\
 & & & & \Leftrightarrow & \left(1+\frac{bP}{k}\right)^{k} & = \lambda \\
 & & & & \Leftrightarrow & 1+\frac{bP}{k} & = \lambda^{\frac{1}{k}} \\
 & & & & \Leftrightarrow & bP & = k\left(\lambda^{\frac{1}{k}}-1\right) \\
 & & & & \Leftrightarrow & P & = \frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)
\end{array}
$$

The $P$-isocline is given by:

$$
\begin{array}{rcccccl}
 & P & = & \omega H\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right) & & & \\
\Leftrightarrow & P & = & 0 & \text{or} & P & = \omega H\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right) \\
 & & & & \Leftrightarrow & H & = \frac{P}{\omega\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right)}
\end{array}
$$

The point $(H_0^*, P_0^*) = (0,0)$ is obviously an equilibrium of the system (95), (96) for any given set of parameters. Under the condition that $\lambda > 1$ another fixed point, $(H^*, P^*)$, exists. It is obtained by intersecting the two isoclines:

$$
\begin{array}{rcl}
H^* & = & \frac{P^*}{\omega\left(1-\left(1+\frac{b\frac{(\lambda^{-k}-1)k}{b}}{k}\right)^{-k}\right)} \\
\Leftrightarrow \quad H^* & = & \frac{P^*}{\omega\left(1-\left(1+\left(\lambda^{\frac{1}{k}}-1\right)\right)^{-k}\right)} \\
\Leftrightarrow \quad H^* & = & \frac{P^*}{\omega\left(1-\lambda^{\frac{1}{k}(-k)}\right)} \\
\Leftrightarrow \quad H^* & = & \frac{P^*}{\omega\left(1-\frac{1}{\lambda}\right)}
\end{array}
$$

The point $(H^*, P^*)$ is an inner equilibrium and is given by $(H^*, P^*) = \left(\frac{P^*}{\omega\left(1-\frac{1}{\lambda}\right)}, \frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)\right)$. The following graphic shows the isoclines and the fixed points of the Nicholson-Bailey model with aggregated search (95), (96). Additionally, vectors are added that represent the dynamics of the system. The vectors stand for the population growth from one generation to the next one. Whether the growth of the host or the parasitoid population is positive or negative is yield by following considerations,

$$
\begin{array}{rcccc}
H'-H & = & \lambda H\left(1+\frac{bP}{k}\right)^{-k}-H & < & 0 \\
& \Leftrightarrow & H\left(\lambda\left(1+\frac{bP}{k}\right)^{-k}-1\right) & < & 0 \\
& \Leftrightarrow & \lambda\left(1+\frac{bP}{k}\right)^{-k}-1 & < & 0 \\
& \Leftrightarrow & \lambda\left(1+\frac{bP}{k}\right)^{-k} & < & 1 \\
& \Leftrightarrow & \left(1+\frac{bP}{k}\right)^{-k} & < & \frac{1}{\lambda} \\
& \Leftrightarrow & \left(1+\frac{bP}{k}\right)^{k} & > & \lambda \\
& \Leftrightarrow & 1+\frac{bP}{k} & > & \lambda^{\frac{1}{k}} \\
& \Leftrightarrow & P & > & \underbrace{\frac{\left(\lambda^{\frac{1}{k}}-1\right)k}{b}}_{H-isocline}
\end{array}
$$

$$
\begin{array}{rcccc}
P'-P & = & \omega H\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right)-P & < & 0 \\
& \Leftrightarrow & \omega H\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right) & < & P \\
& \Leftrightarrow & \omega\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right) & < & \frac{P}{H} \\
& \Leftrightarrow & H & < & \underbrace{\frac{P}{\omega\left(1-\left(1+\frac{bP}{k}\right)^{-k}\right)}}_{P-isocline}.
\end{array}
$$

Hence, these computations yield the following plot:

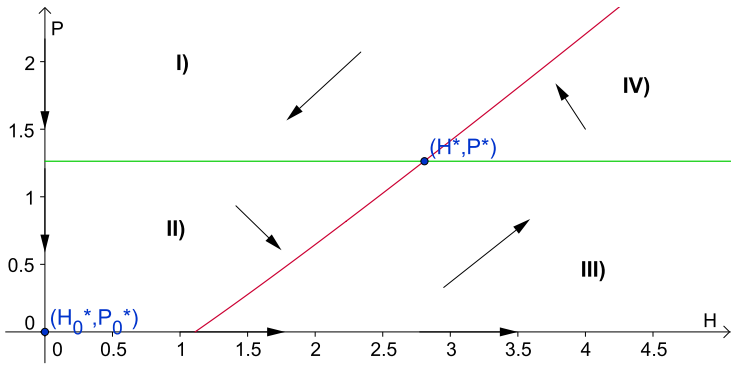



Fig. 45: This figure presents the $H-$ (green) and the $P$-isocline (red) for the parameters $b=1$, $k=0.63$, $\lambda=2$, $\omega=0.9$. The inner fixed point $(H^*,P^*)$ is at $(2.81,1.26)$.

According to the preceding calculations the dynamics in the quadrants I)-IV)

are:

| Quadrant | Dynamic | Biological Meaning |
|---|---|---|
| I) | $H' - H < 0$ and $P' - P < 0$ $\swarrow$ | The host and the parasitoid population are decreasing. |
| II) | $H' - H > 0$ and $P' - P < 0$ $\searrow$ | The host pop. increases while the parasitoid species decreases. |
| III) | $H' - H > 0$ and $P' - P > 0$ $\nearrow$ | The host and the parasitoid pop. increase. |
| IV) | $H' - H < 0$ and $P' - P > 0$ $\nwarrow$ | The host pop. decreases while the parasitoid species increases. |

These results also hold for the case where $k = \infty$, i. e. where $g(x) = \exp(-bx)$.

Now we will focus our attention on the stability properties of the fixed points of (95), (96). A simple stability analysis of $(H_0^*, P_0^*)$ yields that for $\lambda < 1$ this equilibrium is asymptotically stable since we have

$$H' \leq \lambda H \Rightarrow H_t \to 0 \text{ as } t \to \infty$$

$$P' \leq \omega H \Rightarrow P_t \to 0 \text{ as } t \to \infty.$$

Since this is true for any initial condition, $(H_0^*, P_0^*)$ is globally asymptotically stable. In the case of $\lambda > 1$, $(H_0^*, P_0^*)$ becomes unstable. This can be easily seen by the dynamics on the $x$-axes, they lead away from the origin. Formally, this means that system (95), (96) reduces to

$$H' = \lambda H \tag{97}$$

if $P = 0$.
Equation (97) implies

$$H_t \to \infty \text{ as } t \to \infty.$$

In biological terms, equation (97) implies that the host populations will grow exponentially in the absence of parasitism.
For further stability analysis, system (95), (96) will be linearized by calculating the partial derivatives of

$$f_1 := H' = \lambda H \left(1 + \frac{bP}{k}\right)^{-k}$$

and

$$f_2 := P' = \omega H \left(1 - \left(1 + \frac{bP}{k}\right)^{-k}\right)$$

with respect to $H$ and $P$,

$$\begin{aligned}
\tfrac{\delta f_1}{\delta H} &= \lambda \left(1 + \tfrac{bP}{k}\right)^{-k} \\
\tfrac{\delta f_1}{\delta P} &= -\lambda b H \left(1 + \tfrac{bP}{k}\right)^{-(k+1)} \\
\tfrac{\delta f_2}{\delta H} &= \omega \left(1 - \left(1 + \tfrac{bP}{k}\right)^{-k}\right) \\
\tfrac{\delta f_2}{\delta P} &= \omega b H \left(1 + \tfrac{bP}{k}\right)^{-(k+1)}.
\end{aligned}$$

These results form the Jacobian-matrix $Df(x)$, where $f := \begin{pmatrix} f_1 \\ f_2 \end{pmatrix}$ and $x$ is some point in $\mathbb{R}^2$. Hence, the Jacobian matrix for (95), (96) has the following form:

$$D(f(H,P)) = \begin{pmatrix} \lambda \left(1 + \frac{bP}{k}\right)^{-k} & -\lambda b H \left(1 + \frac{bP}{k}\right)^{-(k+1)} \\ \omega \left(1 - \left(1 + \frac{bP}{k}\right)^{-k}\right) & \omega b H \left(1 + \frac{bP}{k}\right)^{-(k+1)} \end{pmatrix}$$

Now the two fixed points will be plugged in the matrix, beginning with $(H_0^*, P_0^*)$,

$$D(f(H_0^*, P_0^*)) = \begin{pmatrix} \lambda & 0 \\ 0 & 0 \end{pmatrix}$$

$$= \lambda.$$

According to Theorem 2.2. the equilibrium $(H_0^*, P_0^*)$ is asymptotically stable for $\lambda < 1$ and unstable for $\lambda > 1$.
In the case of the inner fixed point $(H^*, P^*)$ the Jacobian matrix transforms to

$$D(f(H^*, P^*)) = \begin{pmatrix} \lambda \left(1 + \frac{b\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{k}\right)^{-k} & -\lambda b H^* \left(1 + \frac{b\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{k}\right)^{-(k+1)} \\ \omega\left(1 - \left(1 + \frac{b\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{k}\right)^{-k}\right) & \omega b H^* \left(1 + \frac{b\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{k}\right)^{-(k+1)} \end{pmatrix}$$

$$= \begin{pmatrix} 1 & -bH^*\lambda^{-\frac{1}{k}} \\ \omega(1-\frac{1}{\lambda}) & \omega b H^* \lambda^{-\frac{(k+1)}{k}} \end{pmatrix}.$$

For further investigations concerning the stability of $(H^*, P^*)$ we will take a closer look at the trace and the determinant of $D(f(H^*, P^*))$,

$$\begin{aligned}
\operatorname{tr}(D(f(H^*,P^*))) &= 1+\omega bH^*\lambda^{-\frac{(k+1)}{k}} \\
&= 1+\omega b\frac{\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{\omega\left(1-\frac{1}{\lambda}\right)}\lambda^{-\frac{(k+1)}{k}} \\
&= 1+k\left(1-\lambda^{-\frac{1}{k}}\right)\frac{1}{\lambda}\left(\frac{\lambda}{\lambda-1}\right) \\
&= 1+k\left(1-\lambda^{-\frac{1}{k}}\right)\frac{1}{\lambda-1}
\end{aligned}$$

$$\begin{aligned}
\det(D(f(H^*,P^*))) &= \omega bH^*\lambda^{-\frac{(k+1)}{k}}+\omega(1-\tfrac{1}{\lambda})bH^*\lambda^{-\frac{1}{k}} \\
&= \omega bH^*\lambda^{-\frac{1}{k}}(\lambda^{-1}+(1-\tfrac{1}{\lambda})) \\
&= \omega bH^*\lambda^{-\frac{1}{k}} \\
&= \omega b\frac{\frac{k}{b}\left(\lambda^{\frac{1}{k}}-1\right)}{\omega\left(1-\frac{1}{\lambda}\right)}\lambda^{-\frac{1}{k}} \\
&= k\left(1-\lambda^{-\frac{1}{k}}\right)\left(\frac{\lambda-1}{\lambda}\right)^{-1} \\
&= k\left(1-\lambda^{-\frac{1}{k}}\right)\frac{\lambda}{\lambda-1}.
\end{aligned}$$

The determinant of $D(f(H^*,P^*))$ will be studied more intensively. We will reveal that $\det(D(f(H^*,P^*)))$ is less than one if $k$ is less than one. This is an important result with regard to the Jury criterion.[112] Introduce

$$h(k) := k\left(1-\lambda^{-\frac{1}{k}}\right)\frac{\lambda}{\lambda-1}$$

and differentiate it with respect to $k$. This yields

$$\frac{dh}{dk} = \left(\left(1-\lambda^{-\frac{1}{k}}\right)-\frac{k\lambda^{-\frac{1}{k}}\ln\lambda}{k^2}\right)\frac{\lambda}{\lambda-1} = \left(1-\lambda^{-\frac{1}{k}}\left(1+\frac{\ln\lambda}{k}\right)\right)\frac{\lambda}{\lambda-1}.$$

The derivative of $h$ is greater than zero for every $k>0$, i. e. $h$ is monotonically increasing. We will show this result by using that

$$x-1>\ln x\ \forall x>0, x\neq 1.$$

Now replace $x$ by $\lambda^{\frac{1}{k}}$ and transform

$$\begin{aligned}
& \lambda^{\frac{1}{k}}-1 && > && \ln\lambda^{\frac{1}{k}} \\
\Rightarrow\ & \lambda^{\frac{1}{k}} && > && 1+\tfrac{\ln\lambda}{k} \\
\Leftrightarrow\ & 1 && > && \lambda^{-\frac{1}{k}}\left(1+\tfrac{\ln\lambda}{k}\right) \\
\Leftrightarrow\ & 1-\lambda^{-\frac{1}{k}}\left(1+\tfrac{\ln\lambda}{k}\right) && > && 0.
\end{aligned}$$

[112] See section 2.

Furthermore, note that $h(0) = 0$ and

$$h(1) = \left(1 - \frac{1}{\lambda}\right) \frac{\lambda}{\lambda - 1} = 1.$$

These results imply

$$h(k) < 1 \text{ for } k < 1.$$

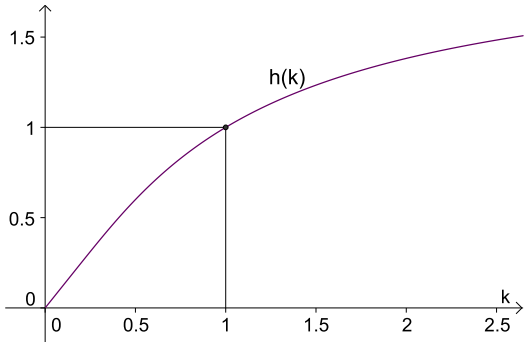



Fig. 46: This figure shows the function $h(k)$ for $\lambda = 5$.

With the help of the preceding results and under the condition that $k$ is less than 1, the following relations are obtained:

$$\begin{aligned}
1 + \operatorname{tr}(D(f(H^*, P^*))) + \det(D(f(H^*, P^*))) &= 2 + k\left(1 - \lambda^{-\frac{1}{k}}\right)\frac{1}{\lambda - 1} + k\left(1 - \lambda^{-\frac{1}{k}}\right)\frac{\lambda}{\lambda - 1} \\
&= 2 + k\left(1 - \lambda^{-\frac{1}{k}}\right)\frac{1}{\lambda - 1}(1 + \lambda) \\
&> 0 \\
1 - \operatorname{tr}(D(f(H^*, P^*))) + \det(D(f(H^*, P^*))) &= k\left(1 - \lambda^{-\frac{1}{k}}\right)\frac{1}{\lambda - 1}(-1 + \lambda) \\
&> 0 \\
\det(D(f(H^*, P^*))) &< 1
\end{aligned}$$

Hence, the Jury criterion proves the inner equilibrium $(H^*, P^*)$ to be asymptotically stable for $k < 1$. In biological terms this means that if the attacks of the parasitoids are sufficiently aggregated, coexistence of the host and parasitoid species is possible.[113] This result is illustrated by the figure below:

[113] Hassell 1991, pp. 572 f.

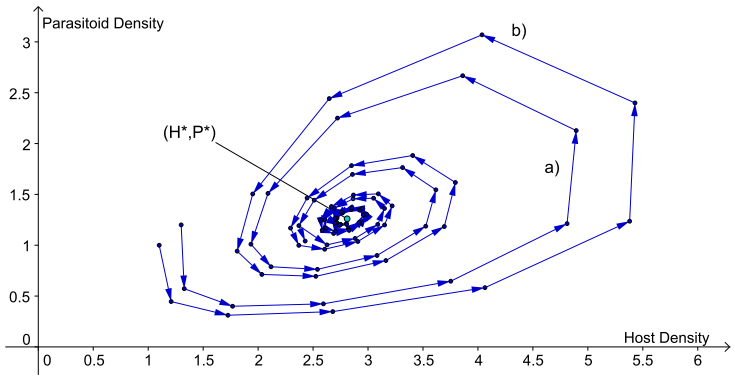



Fig. 47: The figure shows the phase plot of the Nicholson-Bailey model with aggregated search for a given set of parameters, $b = 1$, $k = 0.63$, $\lambda = 2$, $\omega = 0.9$. The inner fixed point $(H^*, P^*)$ of this system is at $(2.81, 1.26)$. The two solutions a) and b) start at the initial conditions $(H_0, P_0) = (1.3, 1.2)$ for a) and $(H_0, P_0) = (1.1, 1)$ for b). The solutions spiral towards the inner fixed point.

The stability analysis of system (91), (92) results in the following bifurcation diagrams for $H^*$ and for $P^*$, respectively. The stability properties (depending on $\lambda$) of $(H_0^*, P_0^*)$ and $(H^*, P^*)$ are visualized using continuous lines (fixed point is stable) and dashed lines (fixed point is unstable).

The chosen parameters are $b = 1$, $k = 0.63$, $\omega = 0.9$.

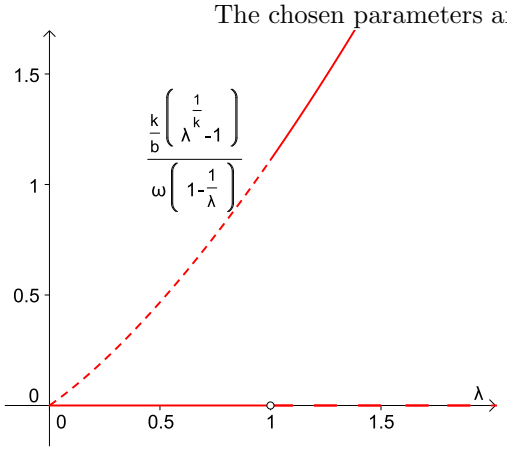



Fig. 48: At $\lambda = 1$ the stability properties of $H_0^*$ and $H^*$ exchange.

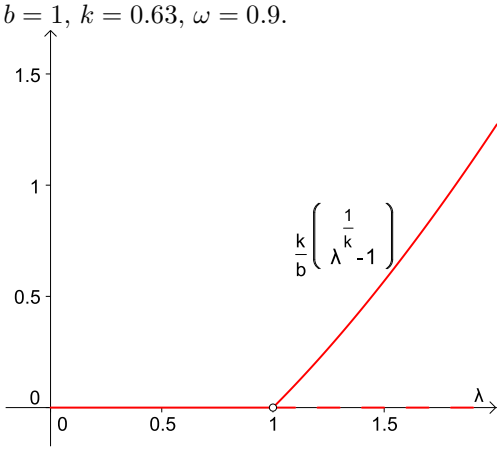



Fig. 49: $P^*$ exists for arbitrary $\lambda > 1$ and is stable.

# 7 Analysis of the Escape Function $g$

We have already encountered the escape function $g$ as a significant part of host-parasitoid models. This chapter treats the derivation of this function. The form of $g$ strongly depends on how one assumes the parasitoids to be distributed among the hosts. Both the Poisson and the negative binomial distribution will be introduced. Poisson distribution, i. e. the case where $g$ has the form of an exponential function, is investigated first since both the original Thompson and the original Nicholson-Bailey use this realization of $g$.[114]
Let again H and H' denote the density of the present and the upcoming host generation, analogously let P and P' represent the present and the future density of the parasitoid species.

## 7.1 Poisson Distribution

First, the derivation of the escape function $g\left(\frac{P}{H}\right) = \exp(-\frac{aP}{H})$ for the generalized Thompson model and $g(P) = \exp(-bP)$ for the generalized Nicholson-Bailey model is given.[115] Therefore, the following assumptions are made:

1. Considering the generalized Thompson model, the average number of parasitoid eggs laid is $aP$. Since these eggs can only be laid in or on a host, $aP$ is at the same time the average number of encounters between the hosts and the parasitoids. The average number of host-parasitoid encounters is given by $bPH$ for the generalized Nicholson-Bailey model. The parameters $a$ and $b$ represent the average number of eggs that each parasitoid lays among the population of hosts and for the parasitoid's search efficiency, respectively.[116] The term $bPH$ results from the assumption that the encounters between parasitoids and hosts obey the law of mass action, which means that the number of encounters between the two species is proportional to the product of

[114] Thompson 1924, pp. 69-89; Nicholson & Bailey 1935, pp. 551-598
[115] Kon 2006, p. 173; Schreiber 2006, p. 719
[116] Getz & Mills 1996, pp. 335 f.; Schreiber 2006, pp. 719 f.

their respective densities.[117]

2. Each host can only be occupied by one parasitoid, i. e. only the first encounter with a parasitoid counts.[118]

3. Parasitoids are randomly distributed on the host population, or more exactly spoken, the parasitoids lay their eggs at random among the host population.[119]

Consequently, the probability of $n$ encounters with parasitoid eggs or parasitoids, respectively, per host follows the Poisson distribution and has the form

$$p(n) = \frac{\exp(-\mu)\mu^n}{n!} \tag{98}$$

where $\mu$ stands for the average number of encounters per host, so $\mu = \frac{aP}{H} = E$ for the generalized Thompson model while for the generalized Nicholson-Bailey model $\mu$ is reduced to $E = bP$. According to the definition of the Poisson distribution the probability of zero encounters per host is given by

$$p(0) = \exp(-\mu) = \exp\left(-\frac{aP}{H}\right) = g\left(\frac{H}{P}\right)$$

or

$$p(0) = \exp(-\mu) = \exp(-bP) = g(P),$$

respectively. Hence, function $g\left(\frac{P}{H}\right)$ or $g(P)$ is represented by the zero-term of the Poisson distribution.[120]

## 7.2 Negative Binomial Distribution

Another realization of the escape function $g$ is obtained when $g\left(\frac{P}{H}\right)$ and $g(P)$, respectively, is set equal to the zero-term of the negative binomial

[117] Elaydi 1999, p. 211
[118] Elaydi 1999, p. 211
[119] Elaydi 1999, p. 211
[120] Elaydi 1999, p. 211

distribution.[121] This means that we replace the Poisson distribution by the negative binomial distribution.
By using the negative binomial distribution the probability of $n$ encounters per host is given by

$$p(n) = \binom{k+n-1}{k-1} q^k (1-q)^n \tag{99}$$

with $q, k > 0$. Thus, the probability of zero encounters is obtained by

$$p(0) = \binom{k-1}{k-1} q^k (1-q)^0 = q^k.$$

Since $\mu = k\left(\frac{1}{q} - 1\right)$ we get $q = \left(1 + \frac{\mu}{k}\right)^{-1}$, where $\mu$ stands for the mean number of encounters per host, so $\mu = \frac{aP}{H} = E$ for the generalized Thompson model while for the generalized Nicholson-Bailey model $\mu$ is reduced to $E = bP$. Hence,

$$p(0) = (1 + \frac{\mu}{k})^{-k} = \left(1 + \frac{aP}{kH}\right)^{-k}$$

or

$$p(0) = \left(1 + \frac{bP}{k}\right)^{-k}$$

is the probability of escaping parasitism for the generalized Thompson and for the generalized Nicholson-Bailey model, respectively.
One can now consider $g(x) = \exp(-\alpha x)$ as a special case of $g(x) = \left(1 + \frac{\alpha x}{k}\right)^{-k}$, where $\alpha$ stands for $a$ or $b$, since[122]

$$\lim_{k\to\infty} \left(1 + \frac{\alpha x}{k}\right)^{-k} = \exp(-\alpha x).$$

We obtained the Poisson distribution in subsection 7.1 because the parasitoids were assumed to be randomly distributed among the hosts. The

[121] May 1978 pp. 835 f.; May 1981, pp. 859-863
[122] Getz & Mills 1996, p. 344

negative binomial distribution is derived by making the following assumptions:[123]

1. The habitat of the hosts consists of several discrete patches.

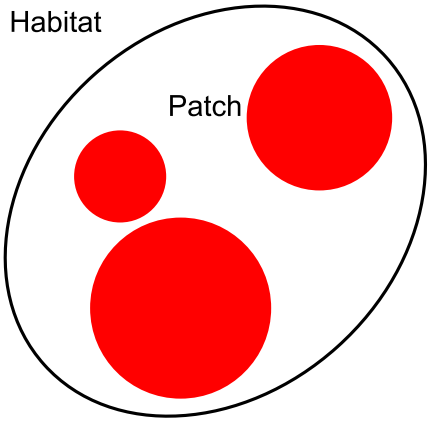



Fig. 50: The ellipse symbolizes the whole habitat of the hosts. The parasitoids are within the different patches.

2. The distribution of parasitoids among these patches obeys the Gamma distribution but is not dependent of the local host density.[124] Therefore, the probability density that a patch includes $x$ parasitoids is given by

$$h(x) = x^{k-1}\frac{\exp(-\frac{x}{\theta})}{\Gamma(k)\theta^k} \tag{100}$$

with $x, k, \theta > 0$ and the Gamma-function $\Gamma(k)$. The parameter $k$ is called the clumping or negative binomial aggregation parameter. It determines the degree of aggregation of parasitic attacks. For increasing $k$ the distribution of parasitoids becomes less and less aggregated. In the special case $k = \infty$, that was investigated in the previous section,

[123] Hassell et al. 1991, pp. 572 f.; May 1978, pp. 835 f.
[124] Hassell et al. 1991, p. 571

the parasitoids are finally completely randomly distributed.[125]

3. Within each patch the parasitoids are randomly distributed.

Further on, it is known that the expected value $M$ and the variance $V$ of the Gamma distribution are

$$M = k\theta \quad \text{and} \quad V = k\theta^2.$$

The probability of zero encounters with parasitoids and thus, escaping parasitism is given by

$$g(z) = \int_0^\infty h(x) \exp(-\alpha x)\, dx$$

assuming that each patch contains $z$ parasitoids on average. This implies $M = k\theta = z \Rightarrow \theta = \frac{z}{k}$. This yields

$$\begin{aligned} g(z) &= \int_0^\infty x^{k-1} \frac{\exp\left(-\frac{x}{\theta}\right)}{\Gamma(k)\theta^k} \exp(-\alpha x)\, dx \\ &= \frac{\left(\frac{1}{\theta}+\alpha\right)^{-k}}{\theta^k} \underbrace{\int_0^\infty x^{k-1} \frac{\exp\left(-x\left(\frac{1}{\theta}+\alpha\right)\right)}{\Gamma(k)\left(\frac{1}{\theta}+\alpha\right)^{-k}} dx}_{=1} \\ &= (1+\alpha\theta)^{-k}. \end{aligned}$$

So, we get

$$g\left(\frac{P}{H}\right) = \left(1 + \frac{aP}{kH}\right)^{-k}$$

[125] May 1978, pp. 335 f.; Schreiber 2006, pp. 720 f.

since

$$\theta = \frac{P}{Hk}$$

and

$$g(P) = \left(1 + \frac{bP}{k}\right)^{-k}$$

since

$$\theta = \frac{P}{k}$$

for the generalized Thompson and the generalized Nicholson-Bailey model, respectively.

Hence, escape function $g$ reduces to the zero term of the negative binomial distribution on the supposition that assumption 1. to 3. are provided.[126]

Remembering the definition of the variance $V$ of the Gamma distribution and substituting $\theta = \frac{P}{Hk}$ or $\theta = \frac{P}{k}$, one obtains

$$V = k\left(\frac{P}{Hk}\right)^2 = \frac{P^2}{H^2 k}$$

and

$$V = \frac{P^2}{k},$$

respectively. So, small values of $k$ lead to large variance, which means that the distribution of the parasitoids is spatially heterogeneous.

On the contrary, for large $k$ there is small variance. In this case the distribution of the parasitoids is rather spatially homogeneous.

In section 6.2 it was shown that spatial heterogeneity stabilizes the Nicholson-Bailey system.[127]

[126] Hassell et al. 1991, p. 571

[127] Getz & Mills 1996, pp. 337, 339; Hassell et al. 1991, p. 573

# 8 Analysis of the Density-Dependent Survival Function $f$

This section provides the derivation and analysis of different choices for the density-dependent survival function $f$. In section 3.2 and 5.1 we already encountered three possible forms of $f$ , namely

- the generalized Beverton-Holt function

$$f(H) = \frac{1}{1 + cH^d},$$

  with $c \geq$, $d > 0$,[128]

- the Ricker function

$$f(H) = \exp(-cH),$$

  with $c \geq 0$,[129]

- the Hassell function

$$f(H) = \frac{1}{(1 + cH)^d},$$

  with $c$, $d \geq 0$.[130]

The Beverton-Holt equation,[131]

$$R(N_t) = \frac{n_1 N_t}{1 + n_2 N_t}$$

with $n_1, n_2 \geq 0$, the Ricker equation,[132]

$$R(N_t) = N_t \exp\left(\frac{r_1}{K}(K - N_t)\right)$$

where $r_1 \geq 0$ and $K > 0$ represent the intrinsic growth rate and the carrying capacity, and the Hassell equation,[133]

$$R(N_t) = \frac{h_1 N_t}{(1 + h_2 N_t)^{h_3}}$$

[128] Schreiber 2006, p. 721
[129] Kon & Takeuchi 2001a, p. 1384; Schreiber 2006, p. 721
[130] Schreiber 2006, p. 721
[131] Getz 1996, p. 2015
[132] Getz 1996, p. 2015; Ricker 1954, pp. 610 f.; Schreiber 2003, p. 203
[133] Getz 1996, p. 2015

with $h_1, h_2, h_3 \geq 0$, equations are used to describe the density of recruitment in fish stocks or insect populations and give the density of recruits in generation $t+1$, denoted by $R(N_t)$.
The term $R(N_t)$ is part of the difference equation describing the density $N_{t+1}$ of a population in generation $t+1$. This equation is given by

$$N_{t+1} = uN_t + R(N_t), \tag{101}$$

where $u$ is the probability of surviving from $t$ to $t+1$. If $u$ equals 0, there are no survivors of generation $t$. Hence, the generations are non-overlapping and the population density in generations $t+1$ is completely determined by the recruits since equation (101) reduces to

$$N_{t+1} = R(N_t).$$

In subsections 8.1 and 8.2 we will assume that $u = 0$.
We denote the density of eggs laid in generation $t$ by $L(0)$ and assume that this density is proportional to the density of the population in generation $t$. Hence,

$$L(0) = lN_t,$$

every individual lays $l$ eggs on the average. Further on, let $L(s)$ denote the density of the larvae (hatched from the laid eggs) at time point $t+s$ where $s$ is the continuous time between two time steps and $0 \leq s \leq 1$. Consequently, we have

$$L(1) = R(N_t). \tag{102}$$

Within a time step the density of larvae can certainly not increase because no eggs are laid between two succeeding time points. Besides, it is not realistic to assume the density of larvae to be constant since factors as intra-specific competition or cannibalism reduce the density of the larvae. Therefore, $L(s)$ is a decreasing function of $s$.

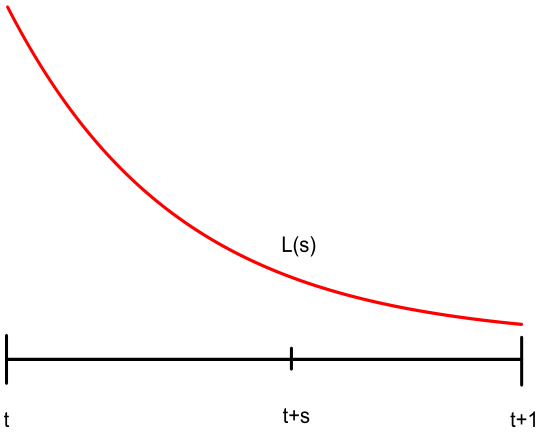



Fig. 51: This figure shows a possible realization of $L$.

In the following subsections, we will derive different outcomes for $R(N_t)$ dependent on the assumptions for the factors influencing the density of the larvae $L(s)$. We will therefore look at the per capita changing rate,

$$\frac{1}{L(s)}\frac{dL(s)}{ds}.$$

Since $L$ is monotonically decreasing, the expression $\frac{1}{L(s)}\frac{dL(s)}{ds}$ yields the per capita death rate.

## 8.1 Beverton-Holt Equation

The Beverton-Holt model was derived by R. Beverton and S. Holt in 1957.[134] In case of the Beverton-Holt equation the per capita mortality rate of the larvae is given by

$$\frac{1}{L(s)}\frac{dL(s)}{ds} = -m_1 - m_2 L(s). \tag{103}$$

The constants $m_1$ and $m_2$ are greater than zero.
The term $m_1$ represents the extrinsic component of mortality. This constant stands for the constant removal of larvae caused by extrinsic factors like predation, weather condition, etc.[135] On the other hand, the constant $m_2$

[134] Beverton & Holt 1965
[135] Beverton & Holt 1965, p. 48

represents the intrinsic or density-dependent component of mortality. We assume that the larvae compete for food, space etc.[136] Therefore, the more larvae there are the higher is the fraction of those dying due to competition.[137] Since we look for $R(N_t)$, we transform (103) to[138]

$$\frac{1}{L(s)(m_1 + m_2 L(s))} \frac{dL(s)}{ds} = -1 \tag{104}$$

and integrate (104) from 0 to 1, i. e. over one time step.
We are able to simplify our calculations by using

$$\frac{1}{L(s)(m_1 + m_2 L(s))} \frac{dL(s)}{ds} = \frac{1}{-m_1} \frac{d\left(\ln\left(\frac{m_1+m_2L(s)}{L(s)}\right)\right)}{ds} \tag{105}$$

since

$$\begin{aligned}
\frac{1}{-m_1} \frac{d\left(\ln\left(\frac{m_1+m_2L(s)}{L(s)}\right)\right)}{ds} &= \frac{1}{-m_1} \frac{1}{\frac{m_1+m_2L(s)}{L(s)}} \frac{L(s)m_2\frac{dL(s)}{ds} - (m_1+m_2L(s))\frac{dL(s)}{ds}}{L(s)^2} \\
&= \frac{1}{-m_1} \frac{L(s)}{m_1+m_2L(s)} \frac{-m_1\frac{dL(s)}{ds}}{L(s)^2} \\
&= \frac{dL(s)}{ds} \frac{1}{L(s)(m_1+m_2L(s))}.
\end{aligned}$$

Now combine (104) and (105) and hence, integrating yields

$$\begin{aligned}
\int_0^1 \frac{d\left(\ln\left(\frac{m_1+m_2L(s)}{L(s)}\right)\right)}{ds} ds &= \int_0^1 m_1 ds \\
\Leftrightarrow \quad \ln\left(\frac{m_1+m_2L(1)}{L(1)}\right) - \ln\left(\frac{m_1+m_2L(0)}{L(0)}\right) &= m_1 \\
\Leftrightarrow \quad \ln\left(\frac{\frac{m_1+m_2L(1)}{L(1)}}{\frac{m_1+m_2L(0)}{L(0)}}\right) &= m_1
\end{aligned}$$

Applying the exponential on both sides results in

$$\frac{\frac{m_1+m_2L(1)}{L(1)}}{\frac{m_1+m_2L(0)}{L(0)}} = \exp(m_1). \tag{106}$$

[136] Beverton & Holt 1965, p. 48; Elaydi 2008, p. 54
[137] Beverton & Holt 1965, p. 48
[138] Beverton & Holt 1965, pp. 48-50

Now use that $L(0) = lN_t$ and transform (106) such that we obtain an expression for $L(1)$,

$$\begin{array}{rcl} \frac{(m_1+m_2L(1))L(0)}{(m_1+m_2L(0))L(1)} & = & \exp(m_1) \\ \Leftrightarrow \quad (m_1+m_2L(1))L(0) & = & \exp(m_1)\times \\ & & \times(m_1+m_2L(0))L(1) \\ \Leftrightarrow \quad m_1L(0)+m_2L(1)L(0) & = & \exp(m_1)m_1L(1) \\ & & +\exp(m_1)m_2L(0)L(1) \\ \Leftrightarrow \quad m_2L(1)L(0)-\exp(m_1)m_1L(1)-\exp(m_1)m_2L(0)L(1) & = & -m_1L(0) \\ \Leftrightarrow \quad L(1)(m_2L(0)-\exp(m_1)m_1-\exp(m_1)m_2L(0)) & = & -m_1L(0) \end{array}$$

$$\Leftrightarrow \quad L(1) \quad = \quad \frac{m_1lN_t}{\exp(m_1)m_1+m_2lN_t(\exp(m_1)-1)}. \tag{107}$$

Since $L(1)$ equals $R(N_t)$, equation (107) can be rewritten as

$$R(N_t) = \frac{n_1N_t}{1+n_2N_t} \tag{108}$$

with

$$n_1 := l\exp(-m_1)$$

and

$$n_2 := l\frac{m_2}{m_1}(1-\exp(-m_1)).$$

Function

$$R(N) = \frac{n_1N}{1+n_2N}$$

is a non-negative, concave and increasing function of $N$ that is bounded by $\frac{n_1}{n_2}$.

- Monotony

  $$\begin{array}{rcl} \frac{dR(N)}{dN} & = & \frac{n_1(1+n_2N)-n_1Nn_2}{(1+n_2N)^2} \\ & = & \frac{n_1}{(1+n_2N)^2} \end{array}$$

  Since $n_1$ is greater than zero by definition, function $R(N)$ is monotonically increasing for $N$ greater than zero.

- Concavity

  $$\frac{d^2R(N)}{dN^2} \quad = \quad \frac{-2n_1n_2}{(1+n_2N)^3}$$

  Since $n_1$ and $n_2$ are positive by definition, the second derivative of $R$ is negative for all non-negative $N$. Hence, $R$ is concave.

- Positivity

  It is easy to see that

  $$R(0) \quad = \quad 0.$$

  Since we just learned that $R$ is monotonically increasing, function $R$ is positive for $N > 0$.

- Boundedness

  $$\begin{array}{rcl} \lim_{N\to\infty} R(N) & = & \lim_{N\to\infty} \frac{n_1 N}{1+n_2 N} \\ & = & \lim_{N\to\infty} \frac{n_1}{n_2} \\ & = & \frac{n_1}{n_2} \end{array}$$

Since $R(N_t)$ equals $N_{t+1}$, function $R$ yields the population density from one generation to the other by iteration,

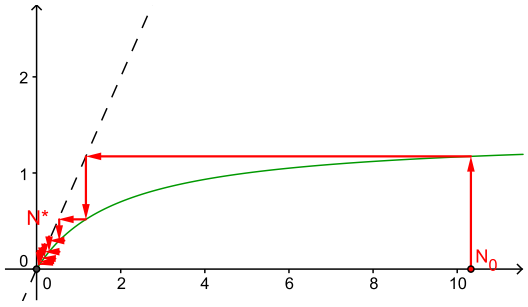
$$N_{t+1} = \frac{n_1 N_t}{1 + n_2 N_t}.$$

For $N_t$ equal to zero the density stays at zero for all $t$. Thus, the origin is a fixed point of $R$. We will obtain another one by the following computation

$$\begin{array}{rcl} 1 & = & \frac{n_1}{1+n_2 N_t} \\ \Leftrightarrow \quad N_t & = & \frac{n_1 - 1}{n_2} = N^*. \end{array}$$

This positive equilibrium only exists for $n_1 > 1$. On the other hand, if $n_1$ is less than 1, the zero-point is the only equilibrium and it is globally asymptotically stable because

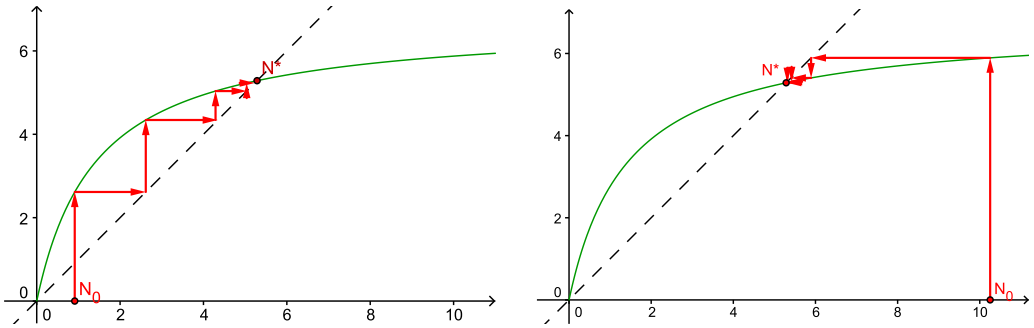
$$\begin{array}{rcl} \frac{d}{dN_t} R(0) & = & \frac{n_1}{1} \\ & = & n_1. \end{array}$$



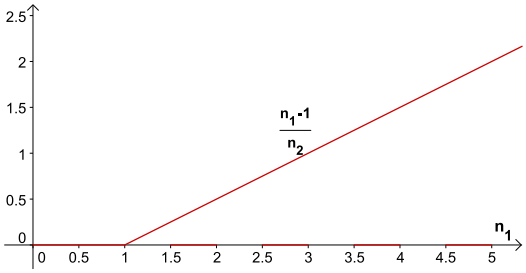
Considering the stability of $N^*$, we get

$$\begin{aligned} \frac{d}{dN_t}R(N^*) &= \frac{n_1}{\left(1+n_2\frac{n_1-1}{n_2}\right)^2} \\ &= \frac{n_1}{n_1^2} \\ &= \frac{1}{n_1}. \end{aligned}$$

Hence, the inner fixed point is asymptotically stable if and only if it exists.[139]




These stability properties are also illustrated in the bifurcation diagram below.




[139] Elaydi 2008, p. 56

Now reconsider the escape function $f(H)$ of the generalized Thompson model. For

$$f(H) = \frac{\lambda H}{1 + cH}$$

we are able to provide much stronger results about the various dynamics of system (10), (11),[140]

$$H_{t+1} = \lambda H_t g\left(\frac{P_t}{H_t}\right) f(H_t)$$

$$P_{t+1} = \omega H_t \left(1 - g\left(\frac{P_t}{H_t}\right)\right) f(H_t).$$

[140] Schreiber 2006, pp. 725 f.

**Theorem 8.1.1.**[141]
*Suppose* $f(H) = \frac{1}{1+cH}$ *with* $c > 0$, $\lambda > 1$ *and T2 holds. Then system (10), (11) exhibits the following dynamics:*

1. *(Parasitoid driven extinction and global stability) If* $\lambda > 1$ *and* $\omega a > \lambda$, *then there exists* $k^* \in (0,1)$ *and* $M > 0$ *such that for* $k > k^*$

$$\lim_{t\to\infty}(H_t, P_t) = (0,0)$$

*whenever* $N_0 > 0$ *and* $P_0 > 0$, *and for* $k < k^*$ *there exists a positive equilibrium* $(H^*, P^*)$ *such that*

$$\lim_{t\to\infty}(H_t, P_t) = (H^*, P^*)$$

*whenever* $H_0 > 0$ *and* $P_0 > 0$.

2. *(Parasitoid failure) If* $\lambda > \omega a$ *and* $k < 1$, *then*

$$\lim_{t\to\infty}(H_t, P_t) = \left(\frac{\lambda - 1}{c}, 0\right)$$

*for any initial condition* $N_0 > 0$ *and* $P_0 > 0$.

3. *(Conditional parasitoid failure) If* $\lambda > 1$, $\lambda > \omega a$, *and* $k > 1$, *then there exists* $y^* > 0$ *and* $M > 0$ *such that*

$$\lim_{t\to\infty}(H_t, P_t) = (0,0)$$

*whenever* $P_0 > y^* N_0 > 0$, *and*

$$\lim_{t\to\infty}(H_t, P_t) = \left(\frac{\lambda - 1}{c}, 0\right)$$

*whenever* $0 < P_0 < y^* N_0$.[142]

These statements directly follow from Theorem 3.2.1. and from the fact that the Beverton-Holt function

$$f(x) = \frac{\lambda x}{1 + cx}$$

[141] Schreiber 2006, pp. 725 f.
[142] Again $y^*$ is the positive solution to $y^* = G(y^*)$, cf. Schreiber 2006, p. 722.

with $c > 0$ has a globally asymptotically stable inner equilibrium for $\lambda > 1$, which is obtained by

$$\begin{array}{rrcl} & x & = & \frac{\lambda x}{1+cx} \\ \Leftrightarrow & 1 & = & \frac{\lambda}{1+cx} \\ \Leftrightarrow & 1+cx & = & \lambda \\ \Leftrightarrow & x & = & \frac{\lambda-1}{c} \end{array}$$

and a globally asymptotically stable equilibrium on the boundary given by

$$x = 0$$

for $\lambda < 1$. These results and those concerning stability have already been investigated above.

## 8.2 Ricker Equation

In case of the Ricker equation the per capita mortality rate of the larvae is given by

$$\frac{1}{L(s)}\frac{dL(s)}{ds} = -m_1(s)N_t - m_2(s). \tag{109}$$

This model was derived in 1954 by William Edwin Ricker.[143] It is, above all, used for describing the development in density of fish populations. It is nevertheless applied on insect species as well.
In contrast to the Beverton-Holt equation (108), described in subsection 8.1, the expressions $m_1$ and $m_2$ are time-dependent. Further on, the per capita mortality rate does not depend on the density of larvae $L(s)$ but on the density of adults $N_t$. The Ricker equation suggests, for example, that shortly after the adults have laid their eggs at time $t$, they feed from their offspring. Hence, $m_1(s)$ represents the mortality due to predation by the own stock or species. In addition to cannibalism, extrinsic factors, e. g. weather conditions, reduce the density of the larvae $L(s)$, represented by $m_2(s)$.[144] Since we look for $L(1) = R(N_t)$, we integrate the per capita death rate over one time step, i. e. from 0 to 1. We use that

$$\frac{1}{L(s)}\frac{dL(s)}{ds} = \frac{d\ln(L(s))}{ds}.$$

[143] Ricker 1954, pp. 559-623
[144] Ricker 1954, pp. 561-563

Then

$$\begin{array}{rcl} \int_0^1 \frac{d\ln(L(s))}{ds} ds & = & -\int_0^1 (m_1(s)N_t + m_2(s))ds \\ \Leftrightarrow \quad \ln(L(1)) - \ln(L(0)) & = & -N_t \underbrace{\int_0^1 m_1(s)ds}_{=:d_1} - \underbrace{\int_0^1 m_2(s)ds}_{=:d_2}. \end{array}$$

Using the properties of the logarithm and applying the exponential function yields

$$\frac{L(1)}{L(0)} = \exp(-d_1 N_t - d_2). \tag{110}$$

Equation (110) is equivalent to

$$L(1) = \exp(-d_1 N_t - d_2) l N_t. \tag{111}$$

Using that $L(1)$ equals $R(N_t)$ and modifying (111) finally gives

$$R(N_t) = N_t \exp\left(\frac{r_1}{K}(K - N_t)\right) \tag{112}$$

with

$$r_1 := \ln(l) - d_2$$

and

$$K := \frac{\ln(l) - d_2}{d_1}.$$

Function

$$R(N) = N \exp\left(\frac{r_1}{K}(K - N)\right)$$

is a non-negative function of $N$ that has am global maximum at $N = \frac{K}{r_1}$.

- Maximum
  First, differentiate $R(N)$ with respect to $N$,

$$\begin{array}{rcl} \frac{dR(N)}{dN} & = & \exp\left(\frac{r_1}{K}(K-N)\right) + N \exp\left(\frac{r_1}{K}(K-N)\right)\left(-\frac{r_1}{K}\right) \\ & = & \exp\left(\frac{r_1}{K}(K-N)\right)\left(1 - \frac{Nr_1}{K}\right). \end{array}$$

  Now set the derivative equal to zero,

$$\begin{array}{rcl} \frac{dR(N)}{dN} & = & 0 \\ \Leftrightarrow \quad \exp\left(\frac{r_1}{K}(K-N)\right)\left(1 - \frac{Nr_1}{K}\right) & = & 0 \\ \Leftrightarrow \quad 1 - \frac{Nr_1}{K} & = & 0 \\ \Leftrightarrow \quad N & = & \frac{K}{r_1} := N_{max}. \end{array}$$

Plugging $N_{max}$ in into the second derivative yields that $N_{max}$ is really a maximum and not a minimum,

$$\begin{aligned} \frac{d^2R(N_{max})}{dN^2} &= \frac{\exp\left(\frac{r_1}{K}(K-N_{max})\right)r_1(N_{max}r_1-2K)}{K^2} \\ &= -\frac{\exp(r_1-1)r_1}{K}. \end{aligned}$$

Since the second derivative of $R$ is negative for $N = N_{max}$, $N_{max}$ is proved to be a maximum.
Besides, we have

$$\exp\left(\tfrac{r_1}{K}(K-N)\right)\left(1-\tfrac{Nr_1}{K}\right) > 0$$

for

$$N < \frac{K}{r_1}$$

and

$$\exp\left(\tfrac{r_1}{K}(K-N)\right)\left(1-\tfrac{Nr_1}{K}\right) < 0$$

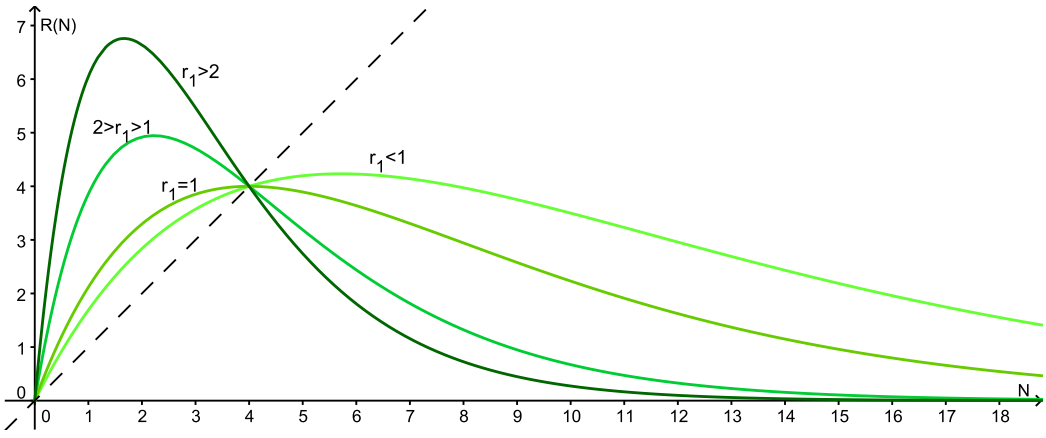
for

$$N > \frac{K}{r_1}.$$

Hence, $N_{max}$ is the global maximum of $R$.

- Positivity
  Since the exponential part of function $R$ is always greater than zero, $R(N)$ is positive for $N$ greater than zero.

Depending on the value of parameter $r_1$ function $R(N)$ slightly differs in form.



Since $R(N_t)$ equals $N_{t+1}$, function $R$ yields the population density from one generation to the other by iteration,

$$N_{t+1} = N_t \exp\left(\frac{r_1}{K}(K - N_t)\right).$$

For $N_t$ equal to zero the density stays at zero for all $t$. Thus, the origin is a fixed point of $N_t$. We will obtain another one by the following computation

$$\begin{array}{rrcl} & 1 & = & \exp\left(\frac{r_1}{K}(K - N_t)\right) \\ \Leftrightarrow & 0 & = & K - N_t \\ \Leftrightarrow & N_t & = & K =: N^*. \end{array}$$

This equilibrium always exists because the carrying capacity $K$ is non-negative. Considering the stability of the two fixed points 0 and $N^*$, we plug them in into the derivative of $R$. Start with the zero-point,

$$\begin{array}{rcl} \frac{d}{dN_t}R(0) & = & \exp(r_1) \times 1 \\ & = & \exp(r_1). \end{array}$$

Hence, the origin is asymptotically stable if and only if $\exp(r_1)$ is less than 1, which is equivalent to

$$r_1 < 0.$$

However, this is impossible since $r_1$ is always assumed to be greater than zero. This implies that the fixed point 0 is never stable. On the other hand, the positive equilibrium $N^* = K$ is asymptotically stable for $r_1$ less than 2 since

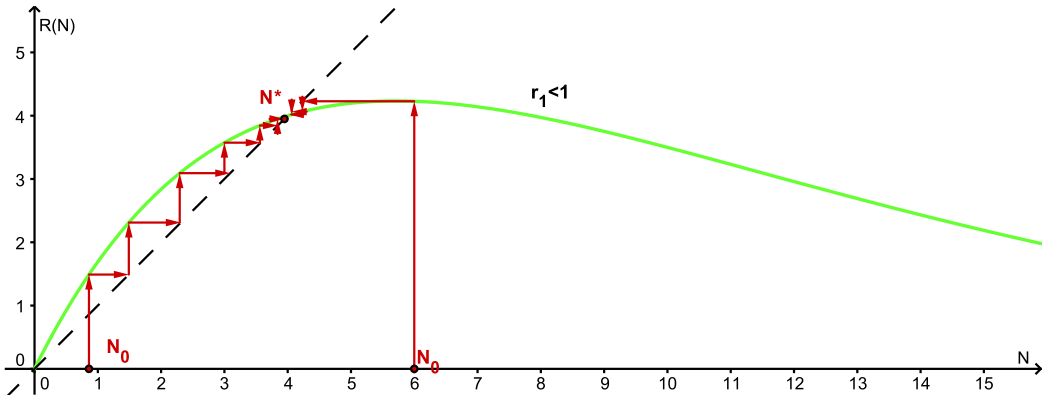
$$\begin{array}{rcl} \frac{d}{dN_t}R(N^*) & = & \exp(0)(1 - r_1) \\ & = & 1 - r_1 \end{array}$$

and since the absolute value of $1 - r_1$ is less than 1 for $0 < r_1 < 2$,

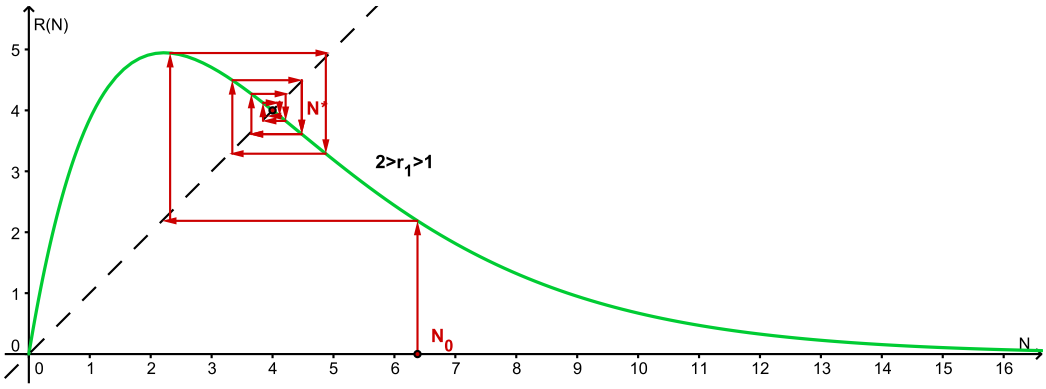
$$\begin{cases} 1 - r_1 < 1 \text{ for } r_1 > 0 \\ -1 + r_1 < 1 \text{ for } r_1 < 2. \end{cases}$$

More exactly spoken, for $r_1$ less than 1 the ascent $1 - r_1 =: \alpha$ of $R$ in the positive fixed point $N^* = K$ is between zero and one, which implies monotone convergence.[145]

[145] Elaydi 2008, p. 57




In the case of $1 < r_1 < 2$ there is oscillating convergence towards the inner equilibrium $N^*$. The ascent $\alpha$ is between $-1$ and 0.




If $r_1$ is even greater than 2, the ascent $\alpha$ is less than $-1$. This implies oscillating divergence from the fixed point $N^*$.

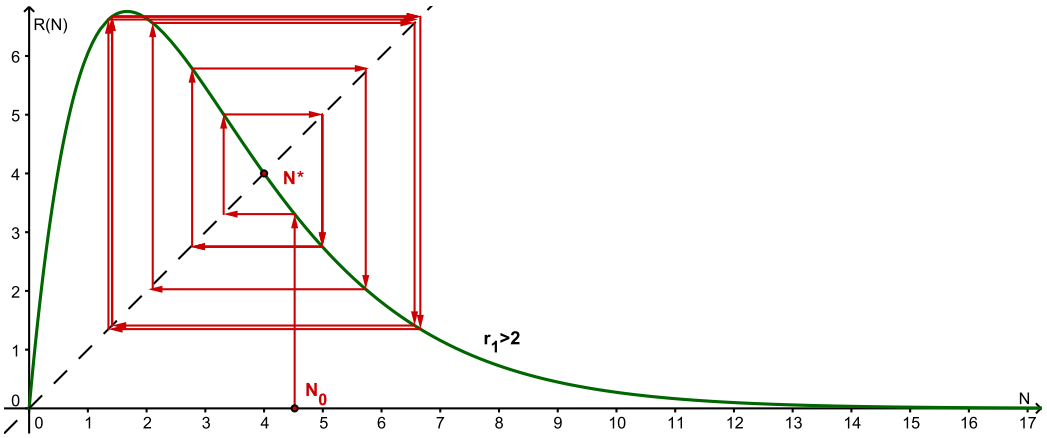



Fig. 52: There exist 2-cycles for $r > 2$.

Considering now $N_{t+2} = R(R(N_t)) = R^{(2)}(N_t)$ reveals some interesting results, that are also important to the considerations made in section 5.2. The form of $R^2$ depends on the parameter $r_1$, as it can be seen below in Fig. 53.

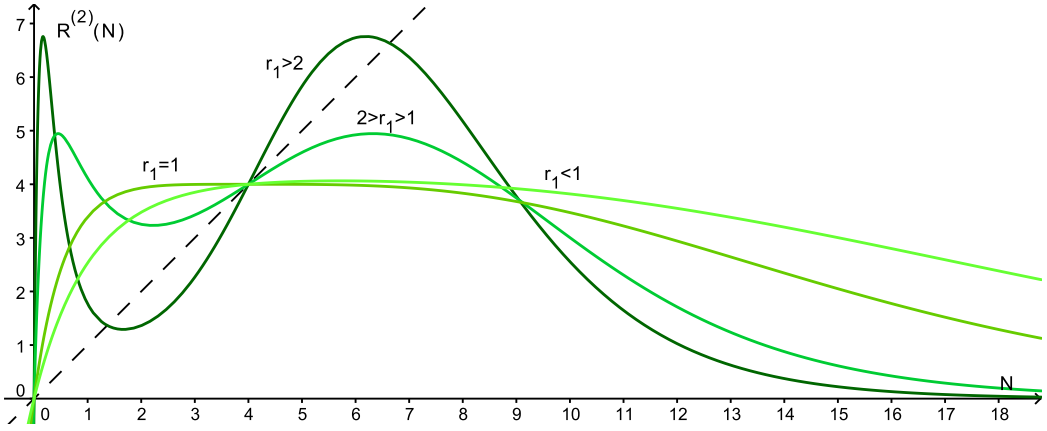



Fig. 53: This figure shows the possible forms of $R^2$.

If we apply $R$ on $N_t$ a second time, there are, of course, the two known fixed points 0 and $N^*$. Those two exist for all iterations $R^{(n)}(N_t)$. Hence, we have

$$\begin{cases} R^{(2)}(0) = 0 \\ R^{(2)}(K) = K = N^*. \end{cases}$$

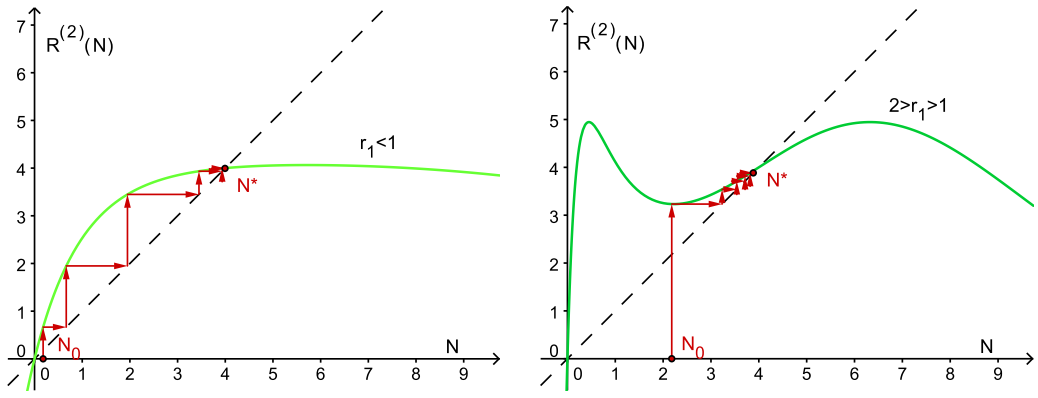
Now we will calculate the ascents of $R^{(2)}$ in the zero point and in $N^*$, denoted by $\alpha_0^{(2)}$ and $\alpha^{(2)}$, respectively.

$$\begin{aligned}\frac{dR^{(2)}(N_t)}{dN_t} &= \frac{dR(R(N_t))}{dR(N_t)}\frac{dR(N_t)}{dN_t} \\ &= \left(\frac{dR(N_t)}{dN_t}\right)^2\end{aligned}$$

If we plug in the two fixed points $N_0^*$ and $N^*$ into the derivative of $R^{(2)}$, we obtain

$$\begin{cases}\alpha_0^{(2)} = \exp(r_1)^2 = \exp(2r_1) \\ \alpha^{(2)} = (1-r_1)^2.\end{cases}$$

Fixed point $N_0^*$ is still unstable for all $r_1 > 0$, while $N^*$ is asymptotically stable for $r_1 \in (0,2)$.




In the case of $r_1 > 2$ the inner equilibrium $N^*$ is unstable while two new fixed points $N_1^*$ and $N_2^*$ of the map $R^{(2)}$ appear. This statement can be shown quickly by using the obtained results of the ascents of $R^{(2)}$ in $N_0^*$ and in $N^*$. Since for $r_1 > 2$ we have that both $\alpha_0^{(2)}$ and $\alpha^{(2)}$ are greater than 1 and because of

$$R^{(2)}(N) = R(\underbrace{R(N)}_{\to 0}) \to R(0) = 0 \text{ for } N \to \infty,$$

the form of the continuous Ricker map implies that there are two more intersections with the 45°-line in addition to the origin and to $N^*$. These two

new fixed points represent a 2-cycle since

$$R(N_1^*) = N_2^* \qquad R(N_2^*) = N_1^*. \tag{113}$$

In order to show this statement suppose that

$$R(N_1^*) = p \neq N_2^*. \tag{114}$$

Then, by applying $R$ a second time and by using that $N_1^*$ is a fixed point of $R^{(2)}$ we obtain

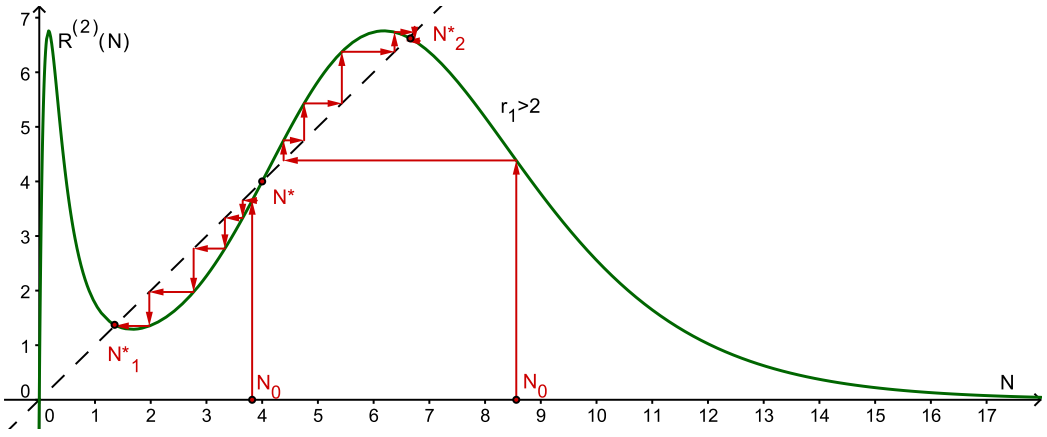
$$R^{(2)}(N_1^*) = N_1^* = R(p). \tag{115}$$

Equations (114) and (115) imply

$$R(N_1^*) = R^{(2)}(p) = p. \tag{116}$$

Hence, $p$ is a fixed point of $R^{(2)}$. Since $p \neq N_2^*$ by assumption and since $p \neq N_1^*$ (otherwise $N_1^*$ would be a fixed point of $R$), $p$ represents a third equilibrium of $R^{(2)}$, which is not possible.
Proceed analogously with $N_2^*$.

As a consequence, the inner equilibria $N_1^*$, $N_2^*$ represent a cycle of period 2. This periodic orbit $(N_1^*, N_2^*)$ is an attractor, as can be seen in Fig. 52. The following figure shows $R^{(2)}$ with $r_1 > 2$ and the 2-cycle.




The 2-cycle loses its stability for $r_1$ greater than 2.5. The more $r_1$ increases the more periodic orbits appear and the periods double with each bifurca-

tion.[146] There exists a critical value $r_c \approx 2.6924$. Up to $r_c$ the interval of stability of the new orbit reduces for factor $4.669\ldots$ with each bifurcation. Value $4.669\ldots$ is called Feigenbaum-constant.[147]

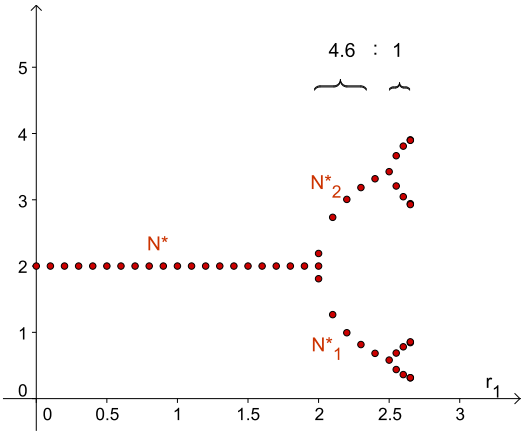



Fig. 54: Here the inner fixed point $N^*$, the 2-cycle $(N_1^*, N_2^*)$ and the 4-cycle can be seen. Only the stable intervals of the orbits are illustrated. Equilibrium $N^*$ exchanges its stability with $(N_1^*, N_2^*)$ at $r_1 = 2$.

Beyond $r_c$ there is an infinite number of cyclic solutions, even orbits of uneven period exist and for most values of $r_1$ there is chaos.[148]

[146] Elaydi 2008, p. 57
[147] Elaydi 1999, p. 40
[148] This plot was done with the support of Raimund Porod.

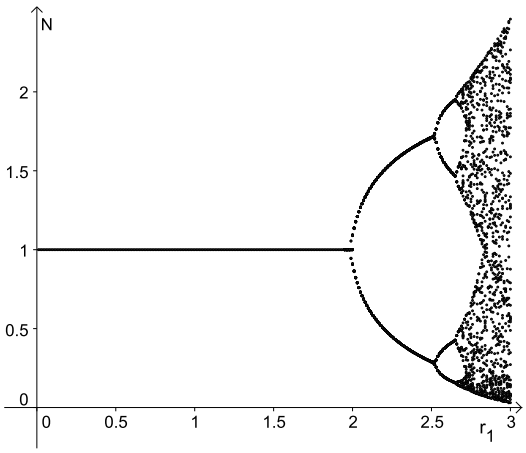



Fig. 55: This figure shows the bifurcation diagram of the Ricker equation for $r_1$ growing up to 3.

Using the Ricker function

$$f(H) = \exp(-cH)$$

as density-dependent survival function in the generalized Thompson model (10), (11),

$$H_{t+1} = \lambda H_t g\left(\frac{P_t}{H_t}\right) f(H_t)$$
$$P_{t+1} = \omega H_t \left(1 - g\left(\frac{P_t}{H_t}\right)\right) f(H_t),$$

we obtain a strong result for the dynamics of (10), (11) under the condition that the parameter $k$ is less than 1:[149]

**Theorem 8.2.2.**
*Assume that $k < 1$ and $f(H) = \exp(-cN)$ is the Ricker survivorship function with $c > 0$. Then there exists an open and dense set of parameters $(\lambda, \omega, a)$ for which there exists a periodic orbit $\mathcal{O}$ (possibly of period 1) such that solutions to (10), (11) satisfy*

$$\lim_{t\to\infty} \operatorname{dist}((H_t, P_t), \mathcal{O}) = 0$$

[149]Schreiber 2007, p. 277

*for an open set of initial conditions* $(H_0, P_0)$ *with full Lebesgue measure.*

The proof of the preceding theorem mainly uses observations of Oleg S. Kozlovski.[150] In other words, Theorem 8.2.3. states that for "most" parameters (in a topological sense) and "most" initial conditions (in a topological and measure theoretic sense), the host-parasitoid dynamics converge towards a periodic orbit. This orbit can possibly be of period one, i. e. it is a fixed point.[151]

[150] Schreiber 2007, pp. 285 f.
[151] Schreiber 2007, p. 277

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# Abstract

The present diploma thesis provides insight into the mathematical modeling of the interaction between a parasitoid population and its host species. The key task of this thesis is to present the derivation and analysis of the Thompson model and the Nicholson-Bailey model as well as possible generalizations. Above all, the work of Kon and Schreiber is used for describing the various dynamics of these systems.
This thesis is divided into eight sections that are described below.

The first section provides some biological introduction to the topic and presents some general models describing host-parasitoid interactions.
Sections 3 and 4 are devoted to the Thompson model and its generalization developed by Schreiber. First, the derivation of this model is discussed. Then this thesis focuses on the different dynamics of the system.
Analogously, sections 5 and 6 treat the analysis of the Nicholson-Bailey model and its generalization, the Beddington model. The work of Kon is used for mathematical analysis.
The mathematical tools needed in section 3 to 6 concerning existence and stability analysis of fixed points, etc. are provided in section 2.
The last two sections are devoted to the so called escape function and the density-dependent survival function. They represent two important factors of the equations describing host-parasitoid interactions.

# Zusammenfassung

Die vorliegende Diplomarbeit behandelt die mathematische Modellierung von Parasitoiden und ihrer zugehörigen Wirtspopulation. Der Fokus dieser Arbeit liegt auf der Herleitung und Analyse des Thompson Modells und des Nicholson-Bailey Modells sowie etwaiger Verallgemeinerungen dieser Modelle. Vor allem werden die Arbeiten von Kon und Schreiber zur Bestimmung der jeweiligen Dynamiken herangezogen.
Diese Dipomarbeit ist in 8 Abschnitte gegliedert, die nun genauer beschrieben werden sollen.

Der erste Abschnitt bietet einen Einblick in den biologischen Hintergrund der Arbeit und führt zugleich allgemeine Modelle für die Interaktionen zwischen Parasitoiden und Wirten ein.
Abschnitt 3 und 4 sind dem Thompson Modell gewidmet. Nach dessen Herleitung, wird eine Verallgemeinerung des Modells eingeführt, das von Schreiber entwickelt wurde. Im Besonderen werden die verschiedenen Dynamiken dieser Verallgemeinerung besprochen.
Analog zum Thompson Modell wird in den Abschnitten 5 und 6 das Nicholson-Bailey Modell erst hergeleitet und anschließend eine seiner bekannten Verallgemeinerungen, das Beddington Modell, erläutert. Mit Hilfe der Arbeiten Kons werden dessen Dynamiken analysiert.
Die für die genannten Analysen benötigen mathematischen Grundlagen werden im zweiten Abschnitt angeführt. Dieser beinhaltet Resultate über die Existenz sowie die Stabilität von Fixpunkten und ähnliches.
Die letzten beiden Abschnitte behandeln die so genannte "escape function" und die "density-dependent survival function". Sie stellen wichtige Faktoren in den Gleichungen dar, die die Wechselwirkungen zwischen Parasitoiden und Wirten beschreiben.

# Curriculum Vitae

## Persönliche Daten

| | |
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| Name: | Carmen Cornelia Lajtos |
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## Ausbildung

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| 1998–2006 | BG Zehnergasse, Wr. Neustadt |
| 2006 | Reifeprüfung mit ausgezeichnetem Erfolg |
| 2006–2010 | Studium der Mathematik an der Universität Wien |
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## Stipendien

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