The predator's numerical and functional responses derived from first principles: population dynamical and evolutionary consequences

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Abstract

This article-based dissertation uses mathematical models to study predator-prey interactions and their population dynamical and evolutionary consequences. The focus is on the predator's numerical and functional response which I derive from first principles, i.e., from the interactions between prey and predator individuals. The aim is to connect population-level phenomena and the long-term evolution of the prey or the predator to processes on the level of the individuals.

The dissertation consists of a general introductory part and three research articles with general results as well as applications to specific models. The first two articles have already been published in the *Journal of Mathematical Biology* and in the *Journal of Theoretical Biology*, respectively. The third article is under review for publication.

In the first research article, I introduce a formal method for the derivation of a predator's functional and numerical response from the interactions between the individual prey and predators. Such derivation permits an explicit interpretation of the parameters and structure of the functional and numerical responses in terms of individual behaviour. The general method is illustrated with several concrete examples. Some examples give novel derivations of already well-known functional responses. Other examples give derivations for responses that have not been used before and lead to a rich population dynamical behaviour including Allee effects as well as simultaneous existence of multiple positive population-dynamical attractors.

In the second research article, I model a stand-off between a predator and a prey individual when the prey is hiding and the predator is waiting for the

prey to come out from its refuge, or when the two are locked in a situation of mutual threat of injury or even death. The stand-off is resolved when the predator gives up or when the prey tries to escape. Using the methods of the first article, this individual-level model leads to the well-known Rosenzweig-MacArthur model but now with parameters that directly connect to the behaviour of the individuals, in particular the giving-up rates of the prey and the predator. I use the model to study the coevolution of the giving-up rates using the mathematical theory of adaptive dynamics. New and different evolutionary results emerge in comparison with the asymmetric war of attrition in evolutionary game theory which is the more traditional way of modelling a stand-off.

In the third research article, I study the evolution of density dependent handling times (i.e., the processing time of captured prey) and the related functional and numerical responses. It is a well-established theoretical result that coexistence of two predator species feeding on one and the same prey is possible, but only if the system exhibits non-equilibrium dynamics. Coexistence is possible because the two predator species occupy different temporal niches: the one with the longer handling time has the advantage when the prey is rare so that holding on to the same catch is the better option, while the species with the shorter handling time has the advantage when the prey is common and easy to catch. Using the adaptive dynamics approach, I show that a predator species with a non-constant handling time that decreases with the prey density is selectively superior regardless of whether the prey is rare or common. The reason is that such generalist predator can occupy both temporal niches all by itself.

By means of these examples, the dissertation demonstrates the strengths of deriving population models from first principles as it enables us to connect population-level phenomena and long-term evolution to the behaviour of the individuals that make up the population.

List of original articles

I   Berardo, C., Geritz, S. A. H., Gyllenberg, M., Raoul, G. (2020). *Interactions between different predator-prey states: a method for the derivation of the functional and numerical response.* Journal of Mathematical Biology, 80, 2431–2468. doi: https://doi.org/10.1007/s00285-020-01500-2

II   Berardo, C., Geritz, S. A. H. (2021). *Coevolution of the reckless prey and the patient predator.* Journal of Theoretical Biology, 530, 110873. doi: https://doi.org/10.1016/j.jtbi.2021.110873

III   Berardo, C., Geritz, S. A. H. (2021). *Analysis of a functional response with prey-density dependent handling time from an evolutionary perspective.* arXiv:2109.15027

Author's contribution

I am the corresponding author of all the articles and I had the leading role in the modelling and analysis as well as in the writing, reviewing and editing of the manuscripts. The scientific articles have not been used in previous dissertations.

Preface

I am infinitely grateful for the past four years spent at the Department of Mathematics and Statistics of the University of Helsinki. My Ph.D. studies have been an extremely important work experience and one of the high points of my life. Along with the development of analytical, problem solving and project management skills, I experienced a high intellectual and personal growth and, as a scientist, I could express the creativity and curiosity that I've treasured since I was little.

I thank my supervisor, Stefan Geritz, for being an enthusiastic teacher and guide in mathematical modelling and adaptive dynamics. Without Stefan's insights and mentorship, this thesis project would have never been completed.

I extend gratitude to Eva Kisdi, who has been a role model woman scientist with her incredible knowledge in biomathematics and high level research. I thank Eva also for organising most of the research group activities, seminars and leisure time.

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I thank the co-authors of my articles and my collaborators, Mats Gyllenberg, Gaël Raoul, Ezio Venturino and Iulia Martina Bulai, for their contribution to my research and the inspiring discussions.

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Huge thanks to my friends, in Italy and Finland, for the life-saving support and the wonderful time together. I also thank all the people met through sport for sharing fun moments and helping me to maintain a balance between work and leisure, in particular the Unpredictables Volleyball people and Puma-Volley people.

My gratitude goes also to Finland, my second home. This country, with its pitch dark winters and never ending summer days, breathtaking landscapes and bizarre activities, contributed to make these years a unique experience.

Last but not least, I am deeply grateful to my family, for the constant support and adaption to my choices. My thoughts are also with those who are not with us anymore.

Helsinki, January 2022
Cecilia Berardo

Contents

Chapter 1

Introduction

The mathematician owns a wonderful tool created by the efforts of many ingenious people, accumulated through the centuries. He has the key that can open a way to the many mysteries of the Universe and obtain, by a few symbols, a synthesis that covers and connects many and diverse results of different sciences.

Vito Volterra (1860-1940)

A mathematical model is a simplified yet interpretable mathematical description of a real phenomenon: *simplified*, because reality is too complex to replicate in full detail, and *interpretable*, for the necessary insight into the mechanisms and interactions to compare the behaviour of the model with that of reality (Geritz and Kisdi 2012).

We use mathematical models mainly to predict and understand the real system that they represent. However, notwithstanding the importance of prediction, Epstein (2008) gives at least sixteen more reasons to use models. Among them, modelling suggests analogies, as it happens that the same equations fit different natural phenomena and apply to a huge range of totally unrelated areas of science.

I am thinking how, for example, similar differential equations have been used in mathematical immunology to simulate the immune response to a disease or a vaccine, or in epidemiology to study how a disease spreads in a population, in economics and mathematical finance to model the bonds and stocks price behaviour and their sensitivity to the interest rate change, in population growth of, for instance, bacteria and other microorganisms.

A simple example is the logistic equation

$$\frac{dn(t)}{dt} = rn(t)\left(1 - \frac{n(t)}{K}\right),$$
(1.1)

where $n(t)$ is the population density at time t. The parameters r and K are the intrinsic growth rate (of the population) and the carrying capacity (of the environment), respectively. The logistic equation has been first used to model population growth by Verhulst (1838) and Pearl and Reed (1920) and later found many applications in, for example, fluid convection (the period doubling cascade in the Rayleigh-Bénard experiment by Libchaber et al. 1982), neuron firing (Crevier and Meister 1998), cardiac arrhythmias (Garfinkel et al. 1992).

With the famous quote of G. Box, *all models are wrong, but some are useful*, Epstein (2008) also argues against the unnecessary disappointment if a model is not exactly *right* (Hutchinson 1961 also shows how some models are most useful when they are wrong). Having said that, a model should still be a fair and close description of the focal phenomena and the modelling approach proposed in this thesis appears as a powerful method to build simple models with an interpretation.

Mathematical modelling of population dynamics dates back through ages and, among the founders, we typically address Malthus, Verhulst, Pearl, Reed, Lotka and Volterra (Edelstein-Keshet 2005, Berryman 1992). The predator-prey model by Lotka (1925) and Volterra (1928) was the first mathematical model to give an abstract explanation of a trophic interaction (Edelstein-Keshet 2005): *why did the predatory fish in the Adriatic Sea increase during the World War I, given that fishing decreased at the time of the war?* The model is composed of the pair of equations

$$\frac{dx(t)}{dt} = \alpha x(t) - \beta x(t) y(t), \tag{1.2}$$

$$\frac{dy(t)}{dt} = \gamma x(t) y(t) - \delta y(t), \tag{1.3}$$

where $x(t)$ and $y(t)$ denote the prey and predator densities at time t, respectively, and α, β, γ and δ are positive parameters describing the interactions between the two populations. One of the most innovative elements of this model was the use of the physical principle of *mass action*, which states that the number of pairwise interactions per unit of time between particles of given kinds in a well-mixed system is proportional to the respective particle densities of both kinds. In the above model the particles are individual prey and individual predators, and their interaction is the prey being captured and killed by the predator. The principle of mass action now has become a standard tool in the mathematical modelling of populations.

The above model also made the biologically unrealistic assumption of a constant *per capita* growth rate of the prey, leading to exponential population growth in absence of the predator. The problem of unbounded

population growth was later fixed by using the logistic growth function in which the *per capita* growth rate decreases at high population densities. However, the meaning of this function in terms of individual-level interactions (birth and death) was still unclear.

In the context of predator-prey models, another major contribution was the introduction of more varied *functional responses* by Holling (1959a,b, 1966), who suggested a non-linear formulation for the predation term, and later by the ratio-dependent equation of DeAngelis et al. (1975) and Beddington (1975). Like in case of the logistic function, the phenomenological approach, also known as *top-down* approach, seemed to be preferred at first, and many functional responses appearing in literature often lacked of an explicit interpretation at the individual level (except for the Holling type II functional response, which was mechanistically derived by Holling 1959a,b via a time budget argument).

Durrett and Levin 1994, among others, raised one of the most important questions in theoretical ecology: *how to scale up from the individual-level behaviours to functions and equations at the population level?* Metz and Diekmann (1986), with their *bottom-up* derivation of the Holling type II functional response from a system of fast time individual state transitions, were among the first ones to claim the potential of the *mechanistic modelling method* (i.e. bottom-up) versus the phenomenological approach and the importance of interpreting the model variables and parameters in terms of the underlying individual-based mechanisms (see also Rashevsky 1959, Sjöberg 1980, Taylor 2013). Later, Geritz and Gyllenberg (2012, 2013, 2014) applied the same method to derive the Beddington-DeAngelis functional response and to show the possible dependence on the predator density of the prey numerical response. Finally, also the logistic equation found several mechanistic explanations (Rueffler et al. 2006 and references therein).

A disadvantage of the mechanistic modelling approach is that, in practice, the model could become rather complex and parameter heavy and therefore often difficult to analyse. Given the rapid development in computing power and numerical methods, one solution is the use of numerical simulations. Alternatively, useful tools to reduce the number of equations and parameters of the model are *time-scale separation*, if the interactions between different individual states happen on different time scales, and *conservation laws*, e.g. when the total population density remains constant on the time scale of the individual state transitions.

All in all, this article-based dissertation investigates the use of mathematical modelling to understand predator-prey interactions and their evo-

lution with a special focus on the mechanistic modelling approach and the functions which describe the biological population at both microscopic and macroscopic level. In the context of climate change and consequent ecological and evolutionary shifts, the interplay between the ecological and evolutionary modelling frameworks is an important tool to study population dynamics. Predator-prey models comprise a simple and well-known tool to understand the mechanistic ecological and evolutionary dynamics of animals and microorganisms. Many theoretical models already proved to be strong frameworks to predict ecosystem responses (Abrams and Matsuda 1997, Yoshida et al. (2003) Koch et al. 2014).

The thesis includes new general results and specific applications which are canonical examples of the methods presented.

The first part of the thesis is introductory and guides the reader through the main research questions, theoretical tools and results. Chapter 2 focuses on the research questions and mathematical methods, such as the *mechanistic modelling approach* and the *adaptive dynamics framework*. Chapter 3 gives an overview on the main results contained in the following articles.

The second part of the thesis is the main body of the dissertation and includes three scientific articles (I-III). Article I serves as an introduction to the mechanistic modelling method applied to predator-prey systems. In addition to some general results, it is shown by means of illustrative examples how explicit modelling of complex interactions between individual prey and predators produces functional and numerical responses, some of which are completely new.

Another and at least as important merit of the mechanistic modelling approach is that the population parameters can be interpreted in terms of individual level processes and, in particular, the rate parameters. As the rate parameters are subject to evolution, this gives a way to study the evolution of the functional and numerical responses, which is the focus of articles II and III.

Articles II and III have similar structure. First, we present the individual level predator-prey interactions and from that derive the functions which describe the population dynamics. Next, we analyse the ecological dynamics, including steady-states, limit cycles and bifurcations. Finally, we study the evolution of the predator-prey interactions using the mathematical framework of adaptive dynamics. Fundamental in this final stage are both analytical and numerical tools, the latter being particularly useful in case of ecological periodic environments.

Chapter 2

Research questions and methods

> *Now, here, you see, it takes all the running*
> *you can do, to keep in the same place.*
>
> Lewis Carroll (1872)

In this chapter, I focus on the research questions addressed in Articles I-III and the mathematical methods applied and developed. In particular, the *mechanistic modelling approach* and the *adaptive dynamics framework*. In the articles, the analysis is conducted also with the use of standard numerical methods and the software *MATLAB*® and *Mathematica*® to numerically integrate the population equations, evaluate convergence of the solutions and give graphical descriptions of the results.

2.1   Research questions

The central research topics addressed in the dissertation are:

Q1 : How to derive functional and numerical responses from first principles in the context of predator-prey models?

Q2 : How do predator-prey strategies coevolve when the predator and its prey enter a stand-off?

Q3 : How does the possibility of evolution of density dependent prey handling affect coexistence of multiple predator species sharing one and the same prey species?

2.2   Mechanistic modelling approach: background motivation

It is well-known that predator-prey interactions are an important driver of adaptive evolution, biodiversity and community ecology (Pettorelli et al. 2015).

While observing predator-prey interactions, the modeller focuses on four key elements: *predation risk*, i.e. the chance for a prey species to be subjected to predation; *prey selection*, i.e. the particular factors that influence how and what prey the predator chooses; the predator *functional response* (Holling 1959a,b, 1966), formally defined as the average number of prey caught per predator per unit of time; the predator and prey *numerical responses*, which include the *demographic* numerical responses, i.e. the growth rates linked to birth and death as functions of the population densities, and the *aggregative* numerical responses, i.e. the rate of change in the populations caused by the predator migration to areas with high prey density (Solomon 1949, Hughes et al. 1973). In particular, functional and numerical responses are the focal object, as they represent the modeller's understanding of the interactions between a specific predator species and its prey, including predation risk and prey selection. Wrong functional and numerical responses can deeply qualitatively affect the predictions on the ecological and evolutionary dynamics.

Functional responses that have been widely used in literature are types I, II and III introduced by Holling (1959a,b, 1966) and the functional response by DeAngelis et al. (1975) and Beddington (1975). Type I assumes a linear dependence between the number of prey eaten per unit of time and the prey density; type II is a hyperbolic function which saturates at a fixed threshold and takes into account the time spent by the predators handling the prey (where *handling time* here stands for the time spent killing the prey, opening the carcass, eating, digesting, but also resting and giving birth); type III is a sigmoid function as the encounter rate of the predator and prey individuals increases monotonically with the prey density; the Beddington-DeAngelis functional response is similar to type II, but contains an extra term in the denominator that is predator density-dependent and was originally interpreted in terms of predator interference.

Biological systems can be way more complex than expected and it is important to find a general method to scale up from specific individual level processes that we observe in nature to population responses. Mechanistic derivations of the main functional responses were given by Metz and Diekmann (1986) and Geritz and Gyllenberg (2012, 2013, 2014), as well

as many works addressed the importance of a mechanistic interpretation of the population functions in both deterministic and stochastic predator-prey models, among them the articles by Jeschke et al. (2002), Johansson and Sumpter (2003), Alexander et al. (2012). The same individual state transitions that determine the functional response can also affect the numerical response and examples of the derivation of numerical responses from fast-time processes have been given by Geritz and Gyllenberg (2013, 2014).
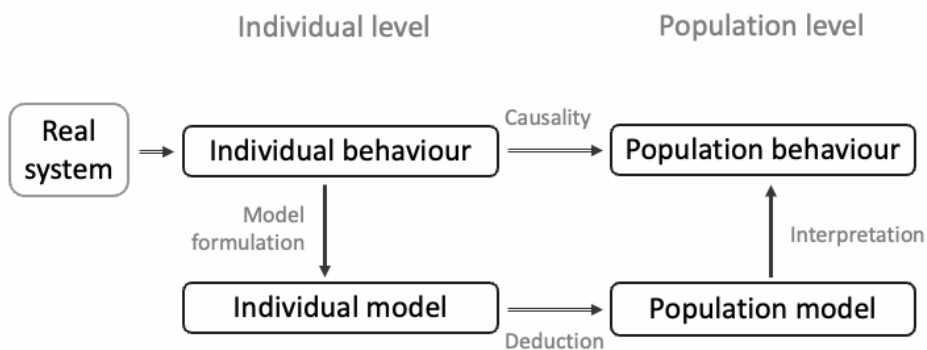

Figure 2.1: Mechanistic modelling method. Illustration inspired by the course *Mathematical modelling* of Stefan Geritz.

2.3   The mechanistic modelling approach

The first step of the mechanistic modelling method (Figure 2.1) requires a deep understanding of the individual states and transitions, with an approach similar to that of compartmental models in epidemiology. In the context of predator-prey models, predators of the same species can be partitioned according to their individual state, such as searching, handling, starving, well-fed, experienced, inexperienced, etc. In the same way, the prey population can be structured according to the individual states like foraging, hiding, or different age or developmental classes such as juvenile or adult, etc.

Individual-level processes can occur on vastly different time scales, some being fast, others being slow. It is typically assumed that birth and death happen on a slow time scale in comparison with more frequent state transitions due to, for example, predation or encounter with other individuals. In

the same way, we could consider the juveniles' lifespan (before maturation into adults) on a slower time scale than interactions, but on a fast time scale if compared to the adults' lifespan (see Lehtinen and Geritz 2019b and Lehtinen and Geritz 2019a).

Once the behavioural states have been specified, the individual-level processes can be described using the same visual form as molecular reactions, where the reactants are the interacting individuals. State transitions can happen spontaneously or may require an interaction with another individual, and they can be visualised as monomolecular and bimolecular reactions, respectively. We apply now the *law of mass action* to convert the individual-level processes into the corresponding population-level equations.

At a later stage, we use *time-scale separation* and the *conservation laws*, to derive the fast time equations and the corresponding equilibrium of the fast dynamics (or *quasi-equilibrium*). At the population level there are as many differential equations as individual states. Since different state transitions may occur on different time scales, the system of differential equations often takes the form of a fast-system with fast changing variables and slow changing variables. Then we can use the method of time-scale separation where we analyse the system on the fastest time scale first in order to calculate the quasi-equilibrium of the corresponding fast variables as functions of the slower variables. This procedure can be repeated for the next fastest time scale and so forth till all equations have been accounted for. The final result is a much smaller system of differential equations for the slowest variables only, but the terms in the equation have become more complicated as they implicitly represent the effects of various fast processes. How this is done in practice is easiest to show in an example.

At this point, we derive the population functions of the predator and the prey following their definitions to build the population equations. In particular, most predator-prey models are special cases of the model by Gause (1934) and Gause et al. (1936)

$$\frac{dx}{dt} = g(x)x - f(x)y, \tag{2.1}$$

$$\frac{dy}{dt} = \gamma f(x)y - \delta y, \tag{2.2}$$

where $f(x)$ is the predator functional response, $g(x)$ is the *per capita* growth rate of the prey in the absence of the predators, i.e. the prey numerical response, $\gamma > 0$ is the *conversion factor* of prey eaten into predator offspring, δ is the *per capita* natural mortality rate of the predators and, finally, $\gamma f(x) - \delta$ is the predators' numerical response.

As a practical example, I consider the predator individuals divided into well-fed (S_1) and starving (S_2) and assume different capture rates, for instance the starving predators have a lower capture rate $c_1 > c_2$ due to exhaustion, or, viceversa, predation increases according to the starvation level and $c_1 < c_2$. I suppose further that after prey capture the predators in state S_1 enter the handling state H_1, and similarly for the predators in state S_2 transitioning into H_2. Ecological factors, such as starvation, can also naturally affect mating (examples are the surface-dwelling hemipteran *Microvelia austrina* by Travers and Sih 1991, or the scorpionfly *Panorpa cognata* by Engqvist and Sauer 2003). Therefore, I suppose different *per capita* fecundities for the well-fed and starving predators $\Gamma_1 > \Gamma_2$, as a little part of the energy gained by the starving predators will be allocated for reproduction (see also the *energy budget theory* by van der Meer 2006, Sousa et al. 2008, Kooijman 2010). I also assume that reproduction happens only in the handling state and the offspring are in the starving state S_2.

The state transitions can be visualised in the following way

(S_1) + (X) $\xrightarrow{c_1}$ (H_1) *the well-fed predator enters the handling state*

(S_2) + (X) $\xrightarrow{c_2}$ (H_2) *the starving predator enters the handling state*

(H_1) $\xrightarrow{d_1}$ (S_1) *from the handling to the well-fed state*

(H_2) $\xrightarrow{d_1}$ (S_1) *from the handling to the well-fed state*

(S_1) $\xrightarrow{d_2}$ (S_2) *from the well-fed state to the starving state*   (2.3)
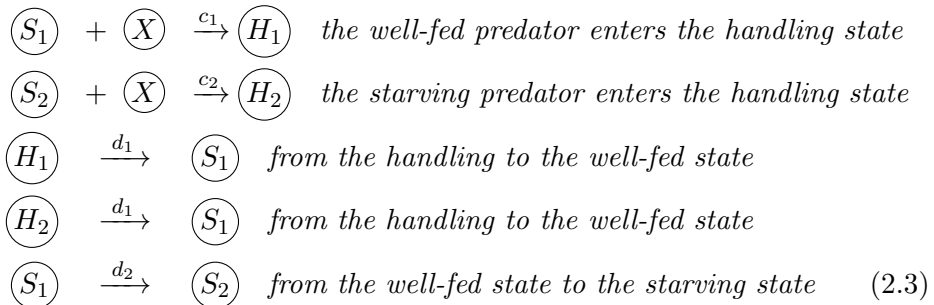
I denote with x and y the total prey and total predator densities. I suppose that the state transitions in (2.3) are on a fast time scale compared to birth and death. I assume further that $g(x, y)$ is the *per capita* growth rate of the prey and δ the *per capita* mortality rate of the predators.

The corresponding population equations on the slow time t become

$$\frac{dS_1}{d\tau} = -c_1 x S_1 + d_1(H_1 + H_2) - d_2 S_1 - \delta S_1, \qquad (2.4)$$

$$\frac{dS_2}{d\tau} = -c_2 x S_2 + d_2 S_1 + \Gamma_1 H_1 + \Gamma_2 H_2 - \delta S_2, \qquad (2.5)$$

$$\frac{dH_1}{d\tau} = +c_1 x S_1 - d_1 H_1 - \delta H_1, \qquad (2.6)$$

$$\frac{dH_2}{d\tau} = +c_2 x S_2 - d_1 H_2 - \delta H_2, \qquad (2.7)$$

$$\frac{dx}{d\tau} = g(x, y)x - (c_1 x S_1 + c_2 x S_2), \qquad (2.8)$$

$$\frac{dy}{d\tau} = \Gamma_1 H_1 + \Gamma_2 H_2 - \delta y. \tag{2.9}$$

As a second step, I apply *time-scale separation* by introducing a small and dimensionless scaling parameter ε and introduce the scaled short time $t = \varepsilon^{-1}\tau$. Since the predators are typically higher up the food chain, assuming that the predator population is much smaller than the prey population is biologically reasonable. This results into dividing the fast-time transition rates by ε and multiplying the predator state variables by ε. The final fast time-scale population dynamics is modelled by the system of equations

$$\frac{dS_1}{dt} = -c_1 x S_1 + d_1(H_1 + H_2) - d_2 S_1, \tag{2.10}$$

$$\frac{dS_2}{dt} = -c_2 x S_2 + d_2 S_1, \tag{2.11}$$

$$\frac{dH_1}{dt} = +c_1 x S_1 - d_1 H_1, \tag{2.12}$$

$$\frac{dH_2}{dt} = +c_2 x S_2 - d_1 H_2, \tag{2.13}$$

$$\frac{dx}{dt} = 0, \tag{2.14}$$

$$\frac{dy}{dt} = 0. \tag{2.15}$$

The system above can be further simplified into three equations by applying the *conservation law* on the total predator density $\frac{dy}{dt} = \frac{dS_1}{dt} + \frac{dS_2}{dt} + \frac{dH_1}{dt} + \frac{dH_2}{dt} = 0$.

As a third step, by setting the equilibrium equations to zero, I compute the asymptotically stable fast-time equilibrium for the fast variables $(\hat{S}_1, \hat{S}_2, \hat{H}_1, \hat{H}_2)$, where

$$\hat{S}_1 = \frac{c_2 x}{d_2\left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)} y, \tag{2.16}$$

$$\hat{S}_2 = \frac{d_2}{d_2\left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)} y,$$

$$\hat{H}_1 = \frac{\frac{c_1 c_2}{d_1} x^2}{d_2\left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)} y,$$

$$\hat{H}_2 = \frac{\frac{c_2 d_2}{d_1} x}{d_2\left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)} y.$$

The functional response is the average number of prey caught per predator per unit of time and, in the particular scenario presented here, it becomes

$$f(x) = \frac{c_1 x \hat{S}_1 + c_2 x \hat{S}_2}{y} = \frac{c_2 x (d_2 + c_1 x)}{d_2 \left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)}, \quad (2.17)$$

that is a special form of the Holling type III functional response $f(x) = \frac{ax + bx^2}{1 + cx + dx^2}$ where the model parameters $a = c_2$, $b = c_1 c_2 \frac{1}{d_2}$, $c = c_2 \left(\frac{1}{d_1} + \frac{1}{d_2}\right)$ and $d = \frac{c_1 c_2}{d_1 d_2}$ now have an interpretation according to the individual transition rates.

In a similar way, given different fecundities for the predator states, the *per capita* reproduction rate of the predators becomes

$$\frac{\Gamma_1 \hat{H}_1 + \Gamma_2 \hat{H}_2}{y} = \frac{c_2 \frac{1}{d_1} x (\Gamma_1 c_1 x + \Gamma_2 d_2)}{d_2 \left(1 + c_2 \frac{1}{d_1} x\right) + c_2 x \left(1 + c_1 \frac{1}{d_1} x\right)}. \quad (2.18)$$

Here the *per capita* reproduction rate corresponds to the product $\gamma f(x)$ in equation 2.2, where the conversion factor $\gamma(x) = \frac{\frac{1}{d_1}(\Gamma_1 c_1 x + \Gamma_2 d_2)}{(d_2 + c_1 x)}$ is no longer constant, but a function of the prey density.

Given different mortality rates δ_i for the predator states, also the *per capita* mortality rate becomes a function of the prey density, that is $\delta(x)$ instead of just δ.

In general, the more assumptions on the state transitions, the more complex the population functions. However, the strength of this method is in the possibility to interpret the population equations in terms of the fast transition rates.

2.4 Adaptive dynamics: background motivation

The modern approach to study evolution is strongly based on the concept of *natural selection* introduced by Darwin (1859).

On one hand, *population genetics* focuses on the genetics (genotypes and genetic interactions), but largely ignores ecology (Crow et al. 1970). *Quantitative genetics* focuses on phenotypes controlled by many different genes each with a small additive effect (Lande 1976, Falconer 1996). Quantitative genetics was in the first place meant to model domestic animal

breeding but later was also used to model phenotypic evolution in ecological systems (see the equation by Lande 1976, as well as many papers by Peter Abrams).

On the other hand, in the context of evolution of phenotypic traits and ignoring genetic detail, highly debated have been the limitations of *optimising selection*, versus *frequency-dependent selection*. A turning point of this discussion was the concept of *eco-evolutionary feedback loop*, integrated by Smith and Price (1973) into their *evolutionary game theory*. Evolutionary game theory is based on frequency-dependent selection and allows for a pay-off function depending on both the individual's strategy and the strategies' distribution.

In the 1990s, the *adaptive dynamics framework* by Metz et al. (1992), Dieckmann and Law (1996), Geritz et al. (1997, 1998, 1999) extended and generalised the idea of frequency-dependent selection from evolutionary game theory to models which allowed for more complex and realistic ecological scenarios. In particular, key concept of adaptive dynamics is the linkage between ecological dynamics and evolutionary dynamics to study the long-term consequences of small mutation in phenotypic traits.

The adaptive dynamics framework is based on four key assumptions (Geritz et al. 1998):

 (i) clonal reproduction;

 (ii) selection happens on a fast time scale, while mutations occur on a slow time scale;

(iii) the density of the mutant trait is small compared to the resident population;

(iv) small mutation steps.

In essence, the resident population with given traits determines the environment, which in turn affects the population dynamics of the resident (ecological feedback loop). The environment generated by the resident trait distribution affects the fitness of a mutant with given different trait values. The mutant fitness determines whether the mutant can invade and affects the final trait composition of the population (eco-evolutionary feedback loop).

With its simplified picture of the eco-evolutionary feedback loop (Figure 2.2), adaptive dynamics provides handy mathematical tools to answer questions such as "What are the conditions that favour certain adaptions?", "How is diversity maintained and how can it be lost?", and among the main

outcomes of the eco-evolutionary dynamics we account for trait substitution, disruptive selection and coexistence of different traits, evolutionary suicide and Red-Queen dynamics (an exhaustive list of references on the main works is provided in the online bibliography by Éva Kisdi https://www.mv.helsinki.fi/home/kisdi/addyn.htm).
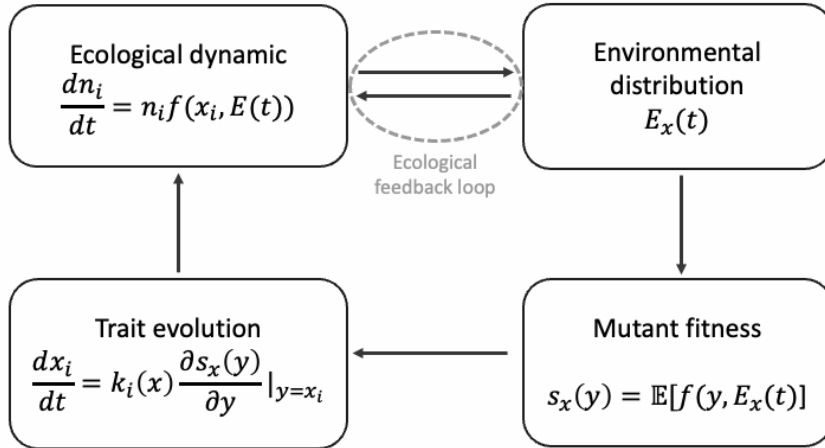

Figure 2.2: Eco-evolutionary feedback loop in adaptive dynamics. Illustration inspired by a talk given by Sebastian Schreiber.

2.5   The adaptive dynamics framework

The adaptive dynamics framework is a rather technical theory built around the key concept of *invasion fitness* defined by Metz et al. (1992).

Consider an ecosystem with $x_1, ..., x_k \in X$ resident strategies (also called traits), where X is the strategy space. The corresponding densities (scalar or vector-valued) are denoted by $n_i, i = 1, ..., k$. I denote with $E(t)$ the *ecological environment* determined by the distribution of the resident traits and $f(x_i, E(t))$ the exponential growth rate of the total population density for strategy x_i.

Assuming that the ecological environment is at an attractor $E_x(t)$ (either a steady state or a periodic attractor), I introduce the mutant strategy $y = x_i + \varepsilon$, where ε is the small mutation step. The invasion fitness is defined as the exponential growth rate of the mutant population with strategy y in the established resident population when the mutant is still rare, i.e.

the long-term average population growth rate

$$s_x(y) = \mathbb{E}[f(y, E_x(t))] = \lim_{t \to 0} \frac{1}{t} \int_0^t f(y, E_x(t))dt. \qquad (2.19)$$

By definition, the invasion fitness verifies $s_x(x_i) = 0$ for all resident strategies at the demographic attractor (defined as *selective neutrality of the residents*). Furthermore, when the environment attains an interior equilibrium the invasion fitness is simply

$$s_x(y) = f(y, E_x(t)), \qquad (2.20)$$

whereas in case of periodic orbit

$$s_x(y) = \frac{1}{t_x} \int_0^{t_x} f(y, E_x(t))dt, \qquad (2.21)$$

where t_x is the period of the resident cycles. In the latter case of convergence to a stable limit cycle, computing the invasion fitness analytically becomes complicated and the use of numerical simulations is often necessary to approximate the orbits.

The sign of the invasion fitness determines the outcome of the invasion. If the fitness is positive, $s_x(y) > 0$, the mutant can invade the resident, and, viceversa, when $s_x(y) < 0$ the mutant dies out.

A rather intuitive result is the *principle of competitive exclusion* in adaptive dynamics which is a direct consequence of the selective neutrality of the residents and states that the dimensionality of the environment at equilibrium in numbers of environmental feedback variables, i.e. the elements of the vector $E_x(t)$, sets a theoretical upper limit to the number of possible coexisting strategies (Levin 1970, Dieckmann and Law 1996, Meszéna et al. 2006).

Another useful result is the *Tube theorem* by Geritz et al. (2002) which formalises the idea of attractor *inheritance* in the context of adaptive dynamics when an invasion successfully occurs. If the mutation step is sufficiently small, then the sum of the densities of the mutant and the resident is close to the resident attractor, being confined in a *tube* in the resident-mutant state space. However, if a sudden change in the resident attractor occurs, such as discontinuous bifurcations leading to multiple attractors (e.g. saddle node bifurcation, homoclinic bifurcation), the mutation step close to the bifurcation point should be infinitely small to keep the mutant strategy on the same side of the bifurcation as the resident strategy. This scenario is unlikely to happen, while possible outcomes are attractor switching, *the resident strikes back* (when the resident switches to a different

attractor that cannot be invaded by the mutant, see Mylius and Diekmann 2001) and *evolutionary suicide* (when the invasion leads to extinction of both the resident and mutant strategies, see Parvinen 2005).

Second key concept in the adaptive dynamics framework is the *selection gradient*, which determines the direction of evolution in the trait space. In particular, the selection gradient is the fitness derivative with respect to the mutant strategy y and evaluated at the resident trait,

$$D(x) = [D_i(x)]_{i=1,...,k}^{\top} = \left(\frac{\partial s_x(y)}{\partial y}\bigg|_{y=x_1}, ..., \frac{\partial s_x(y)}{\partial y}\bigg|_{y=x_k}, \right)^{\top}. \qquad (2.22)$$

The *canonical equation* represents the third key tool of adaptive dynamics and gives a deterministic approximation of the stochastic mutation process by assuming sufficiently small mutations (Dieckmann and Law 1996, Champagnat et al. 2002). The canonical equation describes the rate of change of the evolutionary variable x_i as

$$\frac{dx_i}{dt} = k_i(t)\frac{\partial s_x(y)}{\partial y}\bigg|_{y=x_i} \qquad (2.23)$$

where $k_i(t)$ is a scaling non-negative coefficient which takes into account the *influence of mutation*. In particular, the term $k_i(t)$ is given by the product of the mutation probability per birth event $\mu(x)$, the variance of the mutation step distribution $\sigma^2(x)$ and the effective population size $n_i(x,t)$. While $\mu(x)$ and $\sigma^2(x)$ are basic model ingredients and therefore are given, the effective population size $n_i(x,t)$ can be computed from the resident dynamics.

In case of stable limit cycle for the resident dynamics, defining the effective population size looks more complicated. Ripa and Dieckmann (2013) and Metz et al. (2016) extended the canonical equation to periodic environments. In particular, the rate of change in the variable x_i can be expressed as

$$\frac{dx_i}{dt} = \mu(x)\sigma^2(x)\frac{1}{2}\frac{\int_0^{t_x}(b_i+d_i)dt}{\int_0^{t_x}\frac{(b_i+d_i)}{n_i(x,t)}dt}\frac{\partial s_x(y)}{\partial y}\bigg|_{y=x_i}, \qquad (2.24)$$

where b_i and d_i are the explicit birth term and explicit death term in the population equations for the population type i and the selection gradient is averaged over the length of the limit cycle t_x.

For simplicity, I settle now in the simple case of one-dimensional resident strategy x. When the selection gradient $D(x) > 0$, a mutant with strategy $y > x$ can invade, whereas when $D(x) < 0$, mutants with strategy

$y < x$ will invade. Following the direction given by the fitness gradient, the population evolves until it reaches an *evolutionary singular strategy x^**, such that $D(x^*) = 0$ (i.e. an equilibrium of the canonical equation as the selection gradient vanishes). At the evolutionary singular strategy the fitness landscape has a maximum or a minimum, according to the second derivative of the mutant fitness evaluated at the singular strategy. Alternatively, directional selection may also lead the strategy to the boundary of the strategy space, or to the boundary of viability (evolutionary suicide).

A singular strategy that cannot be invaded by any mutant is called *evolutionary stable* (or ESS, as defined by Maynard Smith 1982 in evolutionary game theory). An ESS satisfies

$$s_{x^*}(y) < 0, \tag{2.25}$$

for all mutant strategies $y \neq x^*$. Moreover, the fitness function has a maximum at the ESS, x^*, and verifies

$$\frac{\partial^2 s_x(y)}{\partial y^2} < 0 \tag{2.26}$$

at the singular strategy.

A singular strategy is called *convergence stable* when a mutant with strategy even closer to the singularity x^* than the resident one can invade, i.e.

$$s_x(y) > 0, \tag{2.27}$$

for $x < y < x^*$ and $x^* < y < x$. Therefore, at the convergence stable strategy the fitness gradient is decreasing and

$$\frac{dD(x)}{dt} = \frac{\partial^2 s_x(y)}{\partial y^2} + \frac{\partial^2 s_x(y)}{\partial y \partial x} < 0. \tag{2.28}$$

A singular strategy can be ESS and convergence stable, or convergence stable but not ESS. In the former case, the singularity is defined *continuously stable strategy* (or CSS by Eshel and Motro 1981; Eshel 1983). In the latter case, two strategies x_1 and x_2 (with $x_1 < x_2$) can mutually invade, i.e. $s_{x_1}(x_2) > 0$ and $s_{x_2}(x_1) > 0$ (with $s_{x_1}(x_1) = 0$ and $s_{x_2}(x_2) = 0$) and give rise to a dimorphism. From the convexity of the fitness function, we deduce that only strategies y such that $y < x_1$ and $y > x_2$ can invade. Therefore the two strategies in the dimorphism gradually become more and more distinct. This phenomenon is called *evolutionary branching* and suggests a possible way to study speciation if applied to sexual populations (see, for example, Kisdi and Geritz 1999 and Geritz and Kisdi 2000).

In order to study evolutionary singularities, a tool that has found several applications is *critical function analysis* (Kisdi 2006, 2015, Geritz et al. 2007). The method is applied to those models with two coevolving parameters, where one evolving variable can be expressed as a trade-off function of the other. The main idea behind critical function analysis is to construct a family of critical functions, each with the critical slope of the trade-off function such that a certain strategy is singular. Thus, the singular strategies are the tangent points of the trade-off function to the critical functions.

Graphical tools are also essential, in particular the *pairwise invasibility plot* (or PIP, see for example Van Tienderen and De Jong 1986, Metz et al. 1995, Kisdi and Meszéna 1993; Kisdi and Meszena 1995) describes the change of sign of the invasion fitness for every combination resident-mutant in the strategy space. The mirror image along the main diagonal of the PIP is called *mutual invasibility plot* (MIP) and gives information on the invasion cone, that is the set of parameter pairs which are mutually invasible. Particularly important are the eight possible configurations of local PIPs near to the singularity given by Geritz et al. (1998). Finally, the *evolutionary tree* describes the mutation and adaption process of the strategies on the slow evolutionary time scale.

In Figure 2.3, I give examples of PIP and MIP based on Article III. In this scenario, the singularity in the PIP is convergence stable but not evolutionary stable, and so a branching point. The diagonal reversed picture in the MIP gives the so called *area of protected coexistence* (i.e. the region denoted with ++), where all pairs of strategies are such that they can mutually invade. Here, the dotted lines (i.e. the c_1-isocline and c_2-isocline) indicate where the selection gradient vanishes in one of the two components and their intersection corresponds to a singular coalition (and, by symmetry, the reciprocal pair below the main diagonal is also a singular coalition).

To conclude this brief introduction to the adaptive dynamics framework, note that the definition of ESS for one-dimensional resident population extends to multi-dimensional resident populations, whereas convergence stability becomes more complicated. In particular, a singular strategy is convergence stable if it is locally attainable and the eigenvalues of the Jacobian matrix for the canonical equation have negative real parts (Dieckmann and Law 1996, Matessi and Di Pasquale 1996, Leimar 2002, 2009). Unlike one-dimensional resident populations where convergence stability is determined by the selection gradient, in multi-dimensional resident populations convergence stability depends on the mutation and variation rates for each resident strategy. In this direction, Leimar (2002, 2009) introduced the

concepts of *absolute convergence stability* (often more demanding for multi-dimensional resident strategies) and *strong convergence stability*, while Hui et al. (2018) used constant mutation rates and step sizes in the canonical equation.
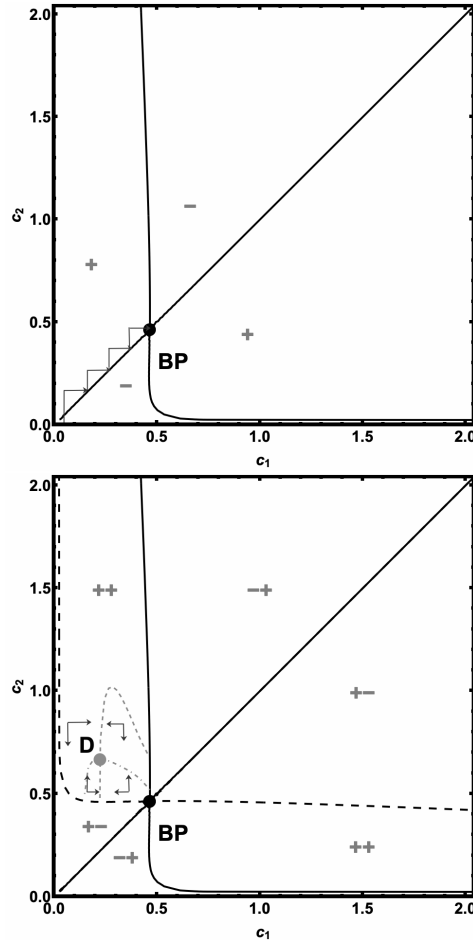
Figure 2.3: Examples of PIP and MIP from Article III.

Top panel: PIP; $+$ and $-$ indicate the sign the invasion fitness $s_{c_1}(c_2)$ of a mutant with strategy c_2 in the environment settled by a resident with strategy c_1; the arrows indicate the direction of evolution (i.e. the *evolutionary path*) and are obtained from the canonical equation; **BP**: branching point (although not immediately obvious on this scale).

Bottom panel: MIP; dashed lines indicate the mirror image of the PIP; the pairs of $+$ and $-$ give the sign of the invasion fitnesses $s_{c_1}(c_2)$ and $s_{c_2}(c_1)$, respectively; $++$: $s_{c_1}(c_2) > 0$, $s_{c_2}(c_1) > 0$, i.e. mutually invasible strategies. $+-$: $s_{c_1}(c_2) > 0$, $s_{c_2}(c_1) < 0$, i.e. invasion and substitution. $-+$: $s_{c_1}(c_2) < 0$, $s_{c_2}(c_1) > 0$, i.e. the mutant strategy cannot invade; the arrows give the evolutionary dynamics in the cone of mutual invasibility; grey dashed line: c_1-isocline, i.e. the selection gradient with respect to c_1 vanishes. Grey dash-dotted line: c_2-isocline, i.e. the selection gradient with respect to c_2 vanishes; **D**: dimorphic singularity.

Chapter 3

Main results

In this Chapter, I list some of the results discovered in the scientific Articles I-III. The main focus of all articles is predator-prey models, and all three use the same mathematical and numerical methods.

I discuss the results in order of the research questions **Q1**, **Q2** and **Q3**. This order corresponds by and large to the order of the articles as well.

3.1 Main results on the mechanistic derivation of functional and numerical responses

Article I gives a new and formal overview of the mechanistic modelling method by considering a predator-prey model with m prey states $\mathbf{x} = (x_i)_{i=1}^m$ and n predator states $\mathbf{y} = (y_j)_{j=1}^n$. The possible state transitions happen spontaneously or due to the encounter of a prey individual for the predators and, viceversa, a predator individual for the prey. The fast time scale equations can be summarised with the system in matrix form,

$$\dot{\mathbf{x}} = (\mathbf{A} + \mathbf{B}(\mathbf{y}))\mathbf{x}, \qquad (3.1)$$
$$\dot{\mathbf{y}} = (\mathbf{C}(\mathbf{x}) + \mathbf{D})\mathbf{y}, \qquad (3.2)$$

where the matrices $\mathbf{A} + \mathbf{B}(\mathbf{y})$, $\mathbf{A}$ and $\mathbf{B}(\mathbf{y})$ in $M_m(\mathbb{R})$ (the $m \times m$-matrix space over $\mathbb{R}$) and $\mathbf{C}(\mathbf{x}) + \mathbf{D}$, $\mathbf{D}$ and $\mathbf{C}(\mathbf{x})$ in $M_n(\mathbb{R})$ (the $n \times n$-matrix space over $\mathbb{R}$) are non-negative off-diagonal matrices and have negative main diagonal entries. Conservation laws apply on the total prey density x

and total predator density y, so that they remain constant on the fast time scale.

In Article I, we discuss the existence and uniqueness of the quasi-equilibrium $(\hat{\mathbf{x}}, \hat{\mathbf{y}})$ and give general definitions for the predator functional response and the numerical responses of the predator and the prey. In particular, we define with β_{ij} the capture rate of a prey in state i by an individual predator in state j and obtain the functional response

$$f(x,y) = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} \beta_{ij} \hat{x}_i \hat{y}_j}{y}. \tag{3.3}$$

In the same way, the prey numerical response is defined as

$$g(x,y) = \frac{\sum_{i=1}^{m} \lambda_i \hat{x}_i}{x} - \frac{\sum_{i=1}^{m} \mu_i \hat{x}_i}{x}, \tag{3.4}$$

with λ_i and μ_i denoting respectively the *per capita* birth and natural mortality rates for the prey in state i. Likewise, the predator numerical response becomes

$$\gamma(x,y)f(x,y) - \delta(x,y) = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} \gamma_{ij} \beta_{ij} \hat{x}_i \hat{y}_j}{y} - \frac{\sum_{j=1}^{n} \delta_j \hat{y}_j}{y}, \tag{3.5}$$

where γ_{ij} is the *per capita* fecundity of the predator in state j feeding on the prey in state i and δ_j denotes the *per capita* mortality rate of a predator individual in state j.

Main result is the general population model where the functions describing the population dynamics depend on both the total prey and predator densities

$$\frac{dx}{dt} = g(x,y)x - f(x,y)y, \tag{3.6}$$

$$\frac{dy}{dt} = \gamma(x,y)f(x,y)y - \delta(x,y)y, \tag{3.7}$$

The equations in (3.6) and (3.7) extend the model by Gause (1934) and Gause et al. (1936) in (2.1) and (2.2).

In this context, we also give concrete applications and derive several new functional and numerical responses from the underlying individual interactions. Among them the mechanistic derivation of the Holling type III functional response, typically associated to prey switching and predator learning (Leeuwen et al. 2007), for which we give two mechanistic interpretations, in terms of different hunger levels and different experience levels of the predators.

In another application, we assume that the predator may overcome the prey defences by causing panic or attacking the isolated individuals and the rate at which the prey leaves its refuge is predator density-dependent. The processes are reminiscent of the individual level interactions introduced by Geritz and Gyllenberg (2012) in their mechanistic derivation of the Beddington-DeAngelis functional response. Here we obtain a functional response that creates an *Allee effect* in the predator dynamics, i.e. at low predator densities almost all prey are protected and cannot be captured (see Allee et al. 1949, Freedman and Wolkowicz 1986, Crawley 1992, Kot 2001, Turchin 2003, Zhu et al. 2003, Bate and Hilker 2014).

In Article I, we also introduce a mechanistic explanation for a functional response with density-dependent handling time, which is further analysed under an evolutionary perspective in Article III. In this case, the predator may either quit the handling state spontaneously or by a chance encounter with a prey individual. This scenario finds several applications in natural ecosystems: it has been observed that visual cues and chemical signals produced by the prey (known as *kairomones*) can affect the behaviour of different predators (a complete list of references for this phenomenon can be found in Article III).

Finally, Article II models from first principles a stand-off between a predator and its prey, when the predator employs predatory techniques to lure its prey, or the prey uses anti-predator strategies to maximise survival, such as deterrent signals, deimatic behaviour, playing dead, physical and chemical features (for a complete list of references, see Article II).

3.2   Main results on the coevolution of predator-prey strategies

Article II investigates question **Q2** and suggests the analysis of a scenario that fits into the research studies on the *ecology of fear* (such as the works by Brown 1999, Brown and Kotler 2007, Katz et al. 2010, 2013, Křivan 1997, 2007).

We assume that the predator and the prey enter a stand-off with a certain probability, upon encounter. The stand-off is resolved either when the predator gives up, or when the prey tries to escape. We define with s and q the giving-up rates of the prey and the predator, respectively, and provide a mechanistic derivation of the corresponding Holling type II like functional response,

$$f_{s,q}(x) = \frac{\beta_{s,q}x}{1 + \beta_{s,q}h_{s,q}x}. \tag{3.8}$$

The capture rate $\beta_{s,q}$ and the handling time $h_{s,q}$ are functions of the fast time state transition rates and, in particular, of the giving-up rates s and q.

Stand-off situations in various specific contexts have been previously studied in evolutionary game theory with the *asymmetric war of attrition*, where two players with unambiguous roles (e.g. owner-intruder, prey-predator) compete for the same pay-off and the winner is determined by its persistence (Smith and Price 1973, Maynard Smith 1974, 1982, Bishop and Cannings 1978, Selten 1980, Kim 1993). As a result of the game, there is no ESS, but a continuum of strict Nash equilibria where one player gives up immediately while the other player can choose any giving-up time above a certain threshold.

In Article II, we apply the adaptive dynamics framework to study the coevolution of the giving-up rates s and q. The main outcomes of our evolutionary analysis appear quite different from the Nash equilibria in evolutionary game theory, namely

(i) the predator gives up immediately (i.e., $q = \infty$), while the prey never gives up (i.e., $s = 0$);

(ii) the predator never gives up (i.e., $q = 0$), while the prey adopts any giving-up rate greater than or equal to a given positive threshold value;

(iii) the predator goes extinct.

In particular, the Nash equilibria in the asymmetric war of attrition cannot be reproduced here and this is a consequence of our modelling approach where the population equations are derived from individual-level interactions with exponentially distributed event times.

The new results reveal the strength of the interplay between the ecological and evolutionary dynamics in the method of analysis. More precisely, the bottom-up modelling approach, to derive the population dynamics from the individual-level transitions, qualitatively affects the evolutionary results.

Moreover, Article II shows that the main costs and benefits for the predator and the prey cannot easily be predetermined as in evolutionary game theory, but are implicit in the births and deaths gained and lost. Only in retrospect, after the model analysis, it became clear, at least in a constant (i.e., non-cycling) population that costs for the predator are measured in terms of the expected time till the next prey capture, while for the prey evolution minimises the predation-related *per capita* death rate (see discussion of Article II).

3.3 Main results on the coexistence of multiple predator strategies

Article III addresses research question **Q3** by focusing on the evolutionary dynamics of one predator's handling time h, when the rate at which the predator's transitions from the handling to the searching state, $bx + c$, has a prey density-dependent part, bx, and a constant part c. Therefore, we express the handling time with the ratio

$$h(x) = \frac{1}{bx + c}. \tag{3.9}$$

This form for the handling time has been derived from first principles in Article I.

Another fundamental assumption concerns the conversion factor of captured prey into predator offspring which depends on the handling time in the following way:

$$\gamma(h) = \int_0^\infty \rho(\tau) e^{-\frac{1}{h}\tau} d\tau. \tag{3.10}$$

In the equation above, $\rho(\tau)$ is the nutrient ingestion rate at τ time units after prey capture in terms of predator offspring per unit of handling time and $e^{-\frac{1}{h}\tau}$ represents the probability that the predator is still handling its prey.

We consider the following generalisation of the model by Rosenzweig and MacArthur (1963) for a single prey species x and potentially multiple predator species with population size $y_i, i = 1, ..., n$

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \sum_{i=1}^{n} \frac{\beta x y_i}{1 + \beta h_i(x)x} \tag{3.11}$$

$$\frac{dy_i}{dt} = \gamma(h_i(x))\frac{\beta x y_i}{1 + h_i(x)\beta x} - \delta y_i, \qquad i = 1, ..., n. \tag{3.12}$$

Main focus of the first part of Article III is on the modelling assumptions for the function $\rho(\tau)$, which acts on the individual level and is linked to the conversion factor $\gamma(h)$ via the inverse of the Laplace transform operator. Central is the bottom-up approach and the main result here regards the mechanistic interpretation of the conversion function in terms of individual-level processes.

Concerning the population dynamics of the model, we find that multiple positive equilibria and multiple stability (of stable cycles and equilibria) are possible outcomes. In this, our model differs from the standard Rosenzweig-MacArthur model.

The second part of Article III analyses the evolutionary dynamics of the prey density-dependent handling time with the adaptive dynamics framework. In this context, previous studies on the coexistence of multiple predator species concluded that a coalition of predator strategies is likely to appear if the resident environment exhibits non-equilibrium dynamics, such as limit cycle or chaos (Koch 1974, McGehee and Armstrong 1977, Levins 1979, Muratori and Rinaldi 1989, Huisman and Weissing 1999, Abrams et al. 2003, Liu et al. 2003, Wilson and Abrams 2004). Other results confirm the assumption that the shape of the predators' functional and numerical responses as functions of the prey density (Armstrong and McGehee 1980) and sufficiently different handling times and conversion factors for each predator type facilitate coexistence (Abrams and Holt 2002).

Unlike the case with fixed handling time studied by Geritz et al. (2007), we find that, in a cycling resident population, if the handling time is a function of the prey density, evolutionary branching and coexistence of different predator strategies are not possible evolutionary outcomes. We also conclude that a predator with density-dependent handling time can invade a convergence stable coalition of two fixed handling times. Therefore, we confirm that a plastic response is a superior strategy than a fixed response in a cycling environment where the predator with density-dependent strategy can adapt to low and high level of prey density by dynamically switching *niche*.

Among the possible evolutionary results, cycles of evolutionary branching and extinction may appear, in case of fixed handling time and for a particular choice of the ingestion rate $\rho(\tau)$. We also find that the dual trait (b, c) evolves to a point where cycles are lost and the population becomes stable. This appears to be a robust outcome. In a wider research context phenomena like this have been called *evolution to the edge of stability* (see Ellner and Turchin (1995), Gragnani et al. (1998), Rinaldi and De Feo (1999), Rai (2004), Rai and Upadhyay (2006), Dercole et al. (2006)).

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