

# Author's Accepted Manuscript

Predation effects on mean time to extinction  
under demographic stochasticity

Gian Marco Palamara, Gustav W. Delius,  
Matthew J. Smith, Owen L. Petchey



[www.elsevier.com/locate/jtbi](http://www.elsevier.com/locate/jtbi)

PII: S0022-5193(13)00279-8  
DOI: <http://dx.doi.org/10.1016/j.jtbi.2013.06.007>  
Reference: YJTBI7343

To appear in: *Journal of Theoretical Biology*

Received date: 2 June 2012  
Revised date: 3 June 2013  
Accepted date: 7 June 2013

Cite this article as: Gian Marco Palamara, Gustav W. Delius, Matthew J. Smith, Owen L. Petchey, Predation effects on mean time to extinction under demographic stochasticity, *Journal of Theoretical Biology*, <http://dx.doi.org/10.1016/j.jtbi.2013.06.007>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

# Predation effects on mean time to extinction under demographic stochasticity

Gian Marco Palamara<sup>1</sup>, Gustav W. Delius<sup>b</sup>, Matthew J. Smith<sup>c</sup>, Owen L. Petchey<sup>1</sup>

<sup>a</sup>*Institute of Evolutionary Biology and Environmental Studies, The University of Zurich, Zurich, Switzerland*

<sup>b</sup>*Department of Mathematics, The University of York, York, United Kingdom*

<sup>c</sup>*Computational Ecology and Environmental Science Group, Microsoft Research, Cambridge, United Kingdom*

## Abstract

Methods for predicting the probability and timing of a species' extinction are typically based on single species population dynamics. Assessments of extinction risk often lack effects of interspecific interactions. We study a birth and death process in which the death rate includes an effect of predation. Predation is included via a general nonlinear expression for the functional response of predation to prey density. We investigate the effects of the foraging parameters (e.g. attack rate and handling time) on the mean time to extinction. Mean time to extinction varies by orders of magnitude when we alter the foraging parameters, even when we exclude the effects of these parameters on the equilibrium population size. Conclusions are robust to assumptions about initial conditions and variable predator abundance. These findings clearly show that accounting for the nature of interspecific interactions is likely to be critically important when estimating extinction risk.

## Keywords:

Trophic Interaction, Predator-Prey Model, Birth and Death Process, Quasistationary Distribution

## 1. Introduction

Population ecologists have long sought to understand how exogenous factors (such as environmental variability) interact with endogenous factors (such as body size, life history, trophic position) to determine the probability that a population will go extinct (Lande and Steinar, 2004). Such insights promise improvements in our understanding of species population dynamics in time and space (Bascompte et al., 1995), in the determinants of ecosystem stability and complexity (McCann, 2000; Allesina et al., 2012), and practical advances in our ability to conserve or eradicate populations (Witting et al., 2000; Liebhold et al., 2003).

Populations can take different routes to extinction. Extinction can occur either through progressive declines in population size, such as due to habitat deterioration, or through sudden crashes in abundance, such as through random catastrophes (Lande et al., 1993). Demographic stochasticity is caused by random variation among individuals in survival and reproduction. Environmental stochasticity is, on the other hand, random variation in the environment, which can lead to changes in the rates of processes influencing population dynamics (such as survival and reproduction rates; Lande and Steinar (2004)). While environmental stochasticity can be important for populations of any size, demographic stochasticity becomes particularly important at low population sizes.

Classical population theory shows that if demographic

stochasticity is the only stochastic process influencing the dynamics of a population then the mean time to extinction increases exponentially with equilibrium population size. In contrast, environmental stochasticity alone can lead to a power law relationship between the mean time to extinction and equilibrium population size (Lande et al., 1993; Foley, 1994). A major body of research to date has sought to understand how the characteristics of individual species influence their probability of extinction. For example, slow life histories and small geographical range sizes are associated with a high extinction risk (Purvis et al., 2000). One outcome of this large body of research is population viability analysis (PVA; Brook et al. (2000)). PVA combines the effects of these different factors to estimate the overall probability that a population will go extinct (Beissinger, 2002; Mace et al., 2008). However the single species models used for assessing population viability often lack the explicit incorporation of direct trophic interactions (Sabo, 2007; Sabo et al., 2008).

Interspecific trophic interactions have been widely studied, theoretically and experimentally, in the fields of population and community ecology. In his pioneering work Holling (Holling, 1959) proposed a simple non-linear relationship between prey density and predator feeding rate, known as the *predator functional response*, that is still widely used today. Since then, various modifications to Holling's original formulation have been made to represent different foraging mechanisms (Real, 1977; Abrams et al., 2000; Jeschke et al., 2002). A general expression for

these is

$$f(n) = \frac{\alpha n^q}{1 + h\alpha n^{q+1}}, \quad (1)$$

where  $\alpha n^q$  is the attack rate (a measure of the encounter rate and capture success of the predator foraging on the prey),  $h$  is the handling time (a measure of the time needed to attack, eat and digest the prey). The attack rate term ( $\alpha n^q$ ) allows for the different scalings of attack rate with prey density that, in combination with the handling time, define the three standard types of functional response:

- Setting  $q = 0$  and  $h = 0$  in expression (1) we obtain the type I functional response. In this case predation rate increases linearly with prey abundance and the predator has a negligible handling time or is able to search and capture prey while handling other prey (Holling, 1965; Jeschke et al., 2004). Type I functional responses are classically associated with filter feeders (Jeschke et al., 2004).
- Setting  $q = 0$  in expression (1) we obtain the type II functional response (Holling, 1959; Real, 1977). The type II functional response is the simplest expression that takes into account the time taken for predators to locate and consume (“handle”) their prey. The type II functional response is classically associated with specialist predators (Turchin, 2003).
- When  $h > 0$  and  $q > 0$  we obtain the type III functional response. The type III has been associated with learning effects of the predator in catching and handling its prey (Real, 1977), with generalist predators switching among alternate prey (Smout et al., 2010) or with spatial effects enabling prey to hide from predators (Vucic-Pestic et al., 2010). Both the type II and III functional responses are characterized by a maximum intake rate ( $1/h$ ) at which predation rate saturates (Holling, 1959).

The effect of the predator functional response on population stability has been widely studied (May, 2001; Drossel et al., 2004). However, such studies have predominantly been conducted using deterministic models (they have also addressed various stability concepts). Nevertheless interspecific interactions are stochastic events. Therefore characteristics of their stochasticity are also likely to influence extinction time. For example, predation pressure could reduce population size and thereby increase the chance of extinction via demographic stochasticity. We should also expect that different predator foraging behaviors will have different effects on a population’s risk of extinction. Most PVAs incorporate the effects of interspecific interactions in population level parameters (Sabo, 2007), for example, predation is included as a constant (density independent) source of mortality rather than a coupled, density dependent population process (Sabo et al., 2008). Single species models used in PVA typically fail to incorporate dynamic interactions between populations and their

predators, which can bias population viability estimates (Sabo, 2007; Sabo et al., 2008).

The stochastic effects of interspecific interactions have also been investigated in multispecies models. Stochastic models of population dynamics range from predator-prey models (McKane et al., 2004) to stochastic food web models (Ebenman et al., 2004; Powell et al., 2009). These models represent trophic-interactions as individual-based reaction probabilities. In cases with large numbers of individuals these models produce macroscopic properties that can be predicted by their deterministic counterparts (McKane et al., 2004; Black et al., 2012). However, the stochastic models can also exhibit properties that cannot be predicted by the deterministic models, for example stochastic resonance (McKane et al., 2005). Extinction rates have also been investigated in predator prey models with linear interaction rates (Parker & Kamenev, 2009). The effects of non linear birth rates on extinction rates have also been studied (Liebhold et al., 2003; Kramer & Drake, 2010). However, to our knowledge, little is known about the effects of the foraging parameters of the functional response on extinction rates.

In this paper we investigate how predation influences the population dynamics of small populations experiencing demographic stochasticity. We aim to clarify the effects of predation on the extinction process. We analyze a single species birth-death process in which the death rate includes density dependent predation by a predator whose abundance is not affected by the abundance of its prey (we explain this assumption below). We then investigate the importance of the predation functional response parameters on the mean time to extinction, and examine the robustness of our results to temporal variation in predator abundance. This investigation is novel in itself, and represents an initial step towards a more complete appreciation of the effects of interspecific interactions on time to extinction.

## 2. Stochastic and deterministic models

We define a single species population as having  $n$  individuals at time  $t$ . We next define functions for the birth rate  $b(n)$  and death rate  $d(n)$  of individuals in the population as

$$\begin{aligned} b(n) &= \lambda \left(1 - \frac{n}{k}\right), \\ d(n) &= \mu + f(n)z, \end{aligned} \quad (2)$$

where  $z$  is the abundance of predators. The logistic form of the birth rate function represents density dependent effects such as intraspecific competition for resources. The parameter  $\lambda$  is the per capita birth rate of the prey species in the absence of density dependence and  $k$  is the maximum possible population size (Nisbet and Gurney, 1982; Näsell, 2001). The death rate includes a constant term

$\mu$ , the predator-free per capita death rate, and the term  $f(n)z$ , the per capita functional response of predation rate to prey abundance (expression (1)). The expected maximum per capita growth rate of the population is then the difference between per capita birth and death rates i.e.,  $r = \lambda - \mu$ . We will keep the per capita birth rate and the predator-free per capita death rate fixed and change the parameters of the functional response in an interval constrained by biological arguments:

- Handling time  $h$  takes values between  $0.001d$  and  $0.1d$ <sup>1</sup>. We assume that  $h$  cannot be larger than the average lifetime of the prey species (assumed to be  $1/\lambda$ ).
- Attack rate ( $\alpha n^q$ ) takes values between  $0.001d^{-1}$  and  $10d^{-1}$ . This choice is justified by empirical observations of foraging behavior of insects and other organisms (Vucic-Pestic et al., 2010; Hammill et al., 2010; Hanski et al., 1991).
- The exponent  $q$  takes values between 0 and 2 again due to empirical observations (Vucic-Pestic et al., 2010) and theoretical work (Williams et al., 2004).
- Predator abundance  $z$  is kept independent from the prey as we aim to study the effect of a generalist predator. In most of our analyses below we fix  $z$  to be constant, the simplest manifestation of the assumption that predator abundance is independent of prey abundance, as has been assumed for generalist predators in previous studies (e.g. Hanski et al. (1991)). In this case, when the growth parameters  $\lambda$ ,  $\mu$  and  $k$  are fixed, the relevant parameters for the dynamics are  $\alpha z$  and  $h/z$  (see appendix A). Later, we relax the assumption that  $z$  is constant and allow it to fluctuate (details below). We choose  $z$  to take values between 1 and  $k$ .

We combine expressions (1) and (2) to obtain expressions for the population birth and death rates,  $B(n)$  and  $D(n)$ , respectively as

$$\begin{aligned} B(n) &= nb(n) = n\lambda \left(1 - \frac{n}{k}\right), \\ D(n) &= nd(n) = n\mu + \frac{\alpha zn^{q+1}}{1 + \alpha hn^{q+1}}. \end{aligned} \quad (3)$$

The state of the system can be characterized by the probability  $p(n, t)$  of having  $n$  individuals at time  $t$ , where  $n$  takes integer values in the range  $\{0, \dots, k\}$ . The master equation describing the time evolution of the probability distribution is

$$\begin{aligned} \frac{dp(n, t)}{dt} &= D(n+1)p(n+1, t) + B(n-1)p(n-1, t) \\ &\quad - (B(n) + D(n))p(n, t). \end{aligned} \quad (4)$$

In order to express equation (4) in a compact way we defined  $p(k+1, t) = p(-1, t) = 0$ . Given an initial probability distribution  $p(n, 0)$ , equation (4) uniquely determines the probability distribution at later times. The process represented in this master equation always ends up with population extinction, represented as the stationary distribution  $\bar{\mathbf{p}} = (1, 0, \dots, 0)$ , which the distribution  $p(n, t)$  approaches as time  $t$  approaches infinity. This is because, given sufficient time (which may be extremely large when populations are large) stochastic fluctuations in the population size will eventually, at some time, cause the population size to be zero. Since there is no immigration in this model the population cannot recover from that state. In section 2.2 we will show how to compute the probability of having a population of size  $n$  at time  $t$  conditioned on the fact that it has not yet gone extinct.

### 2.1. Deterministic rate equation

A deterministic rate equation, describing the time evolution of the mean population size, can be associated to every stochastic birth and death process (Gardinier, 2009). The deterministic equation is given by

$$\frac{dn}{dt} = B(n) - D(n). \quad (5)$$

In our case, substituting the rates (3) into equation (5), we obtain

$$\frac{dn}{dt} = \lambda n \left(1 - \frac{n}{k}\right) - \mu n - \frac{\alpha zn^{q+1}}{1 + \alpha hn^{q+1}}. \quad (6)$$

In order to understand the roles of deterministic versus stochastic effects in prey extinction we compute the fixed points of equation (6) and their stability. We use as measure of stability the real part of the leading eigenvalue of the Jacobian matrix evaluated at each fixed point (hereafter termed the stability coefficient, detailed in appendix A). Mean population numbers close to the value of an unstable fixed point evolve away from the fixed point value while those close to a stable fixed point value evolve towards that value.

### 2.2. Deterministic and stochastic effects on extinction

In equation (6) the extinction state  $n = 0$  is always a fixed point, while the other fixed points are given by the intercepts between the per capita growth term ( $r - \lambda n/k$ ) and the per capita functional response  $zf(n)$  (see figure 2). Two different extinction scenarios are revealed by the analysis of the deterministic equation, associated with changes in the stability of the extinction state (Assaf et al., 2010).

When  $q = 0$  and  $h > 0$  (type II functional response) the extinction state can be stable or unstable. A stable extinction state indicates that when the population size is sufficiently close to zero the birth-death process (3) causes the mean population size to tend towards zero because the mean population death rate exceeds the mean birth

<sup>1</sup>The unit of measure of time is arbitrarily set to days (d).



rate. In contrast, an unstable extinction state indicates that when the mean population size is sufficiently close to zero the population size tends away from zero, and demographic stochasticity is necessary for the population to go extinct. If  $\alpha_p = z\alpha > r$ , the extinction state is stable. In this case there are two positive fixed points, one stable and one unstable, or no positive fixed points (see figure 1). At  $\alpha_p = r$  there is a transcritical bifurcation, at which the unstable fixed point goes to 0 (see figure 1) and the extinction state becomes unstable. When the extinction state is unstable ( $\alpha_p < r$ ) there is only one other fixed point and this is stable (see figure 1).

When  $q > 0$  and  $h > 0$  (type III functional response) the model has at most three non zero fixed points and the extinction state will always be unstable. In contrast to the type II functional response, for  $q > 0$  there are combinations of foraging parameters for which there can be up to three non zero fixed points (see appendix A). In this case two of the three non-zero fixed points are stable and one is unstable (see figure 1).

Given the birth and death process (3), extinction is caused by demographic stochasticity and typically occurs in two different ways depending on whether the extinction state is a stable or unstable fixed point of the deterministic rate equation (6). For the type II functional response, below the transcritical bifurcation, extinction is caused by a large fluctuation which brings the system from the stable to below the unstable fixed point. From there a fast deterministic evolution takes the population quickly to the stable extinction state. For the type II functional response after the bifurcation, and for the type III functional response, extinction is caused by a large fluctuation in density which brings the system from the stable fixed point to the unstable, absorbing extinction state. For the type III functional response when there are two stable fixed points and the population is near the larger stable fixed point, extinction needs two large fluctuations to occur, one fluctuation which brings the system from the larger to the lower stable fixed point and another fluctuation which brings the system from the lower stable fixed point to the unstable extinction state.

### 2.3. Quasistationary distribution (QSD) and mean time to extinction (MTE)

When the deterministic rate equation has at least one stable fixed point, the system approaches a quasi stationary state with a time independent distribution  $\pi(n)$ ; this is called the *Quasistationary Distribution* (Bartlett, 1960; Nisbet and Gurney, 1982). The quasistationary distribution  $\pi(n)$  is obtained from the probability  $p_c(n, t)$ , that of finding  $n$  individuals at time  $t$ , conditioned on the fact extinction has not occurred yet:

$$p_c(n, t) = \frac{p(n, t)}{1 - p(0, t)}. \quad (7)$$

We derive a master equation for the conditioned probability  $p_c(n, t)$  and look for its stationary solution  $\pi(n)$  (see appendix B). When the initial condition (the probability  $p_0(n)$  of finding  $n$  individuals at time 0) of equation (4) is set to the quasistationary distribution, then the probability of finding  $n$  individuals at time  $t$  becomes

$$p(n, t) \simeq \pi(n) \exp(-t/MTE). \quad (8)$$

The time to extinction is then an exponentially distributed random variable with mean equal to the MTE and,

$$MTE = \frac{1}{D(1)\pi(1)}. \quad (9)$$

There are more complicated expressions for the mean time to extinction when the initial condition is not the quasi stationary distribution  $\pi(n)$  (see appendix B). We found the time for the system to reach the quasistationary distribution is negligibly small compared to the MTE. We compute the MTE of the birth and death process (3) for different functional responses and for different values of the foraging parameters within the functional responses. All other parameters remain fixed.

### 2.4. Numerical calculations

It is not possible to obtain closed expressions for the quasistationary distribution  $\pi(n)$  of the birth and death process (3). Instead we obtain the quasistationary distribution in a realistic range of foraging parameters by an iterative numerical scheme described in appendix B. In order to perform numerical calculations we fix the growth parameters of equation (6) in the following way:  $\lambda = 1.5 d^{-1}$ ;  $\mu = 0.5 d^{-1}$ ;  $k = 150$ . With that choice the intrinsic growth rate of the prey population is fixed to  $1 d^{-1}$ . In the absence of predators i.e., setting  $z = 0$  in equation (6), the model has a non zero fixed point at  $n_0 = kr/\lambda = 100$ .

We compute the logarithm of the MTE of the birth and death process (3) obtained using the quasi stationary distribution as initial condition (see appendix B) for different combinations of foraging parameters. The foraging parameters of the functional response affect the MTE in direct and indirect ways. The foraging parameters affect the MTE indirectly by influencing the equilibrium population size of the prey. They influence it directly by changing the MTE even for a fixed equilibrium prey population size. In order to isolate the effect of the shape of the functional response (direct effect) from the effect of the fixed point population number  $n_0$  (indirect effect), we keep  $n_0$  unchanged. This imposes the following relation between the attack rate parameter  $\alpha$  and the handling time parameter  $h$ :

$$\alpha_q = \frac{\alpha(h, n_0)}{n_0^q} = \frac{rk - \lambda n_0}{n_0^q [zk - hn_0(rk - \lambda n_0)]}. \quad (10)$$

In order to avoid fixing an unstable equilibrium with relation (10), we limit our investigation to those values of

handling time which give rise to a stable fixed point (see appendix A) i.e.,

$$h < h_1 = \frac{\lambda z k [(1 - q) \lambda n_0 + q r k]}{n_0 (1 + q) (r k - \lambda n_0)^2}. \quad (11)$$

As the handling time approaches the value

$$h_0 = \frac{z k}{n_0 (r k - \lambda n_0)}, \quad (12)$$

the required attack rate approaches infinity, so we limit ourselves to  $h < \min(h_0, h_1)$ . In the case of  $q > 0$  we also keep  $h$  small enough so that we do not enter the bistable region. Matlab code to reproduce our calculations can be found at [http://purl.org/net/extinction\\_code](http://purl.org/net/extinction_code).

### 2.5. Temporal variation in predator abundance

Finally, we explored the effects of variation in predator abundance on the MTE. Here we do not have a closed expression for the MTE of the prey but we can simulate many replicates of the birth and death process (3) using the Gillespie algorithm (Gillespie, 1977) and compute the MTE numerically. The assumption of constant predator abundance was relaxed by allowing  $z$  (predator abundance) to vary randomly through time, with values drawn from a uniform distribution  $[z - z/2, z + z/2]$ , where separate investigations were performed for  $z = 2, 10, 50$ . We then explored the effects of seasonal variation in predator abundance on the MTE of the prey. Periodic forcing was introduced by setting

$$z = z_0 (1 - \sin(\omega t)), \quad (13)$$

where  $z_0$  is the amplitude and  $\omega$  is the frequency of the forcing. We performed separate investigations for  $z_0 = 2, 10, 50$  and with  $\omega = 0.1, 0.02, 0.01$ .

## 3. Results

The MTE of the model without predation is extremely large ( $10^{25}d$ ), meaning that extinction will almost certainly never occur. When there are predators, changes in the attack rate ( $\alpha$ ), the handling time ( $h$ ) and the scaling of attack rate ( $q$ ) strongly influences the MTE through changes in equilibrium population size. These indirect effects on the MTE can be seen in figure 3. As expected, the MTE is relatively low when the functional response parameters lead to deterministic extinction (region labeled  $n_0 = 0$  in figure 3). When the foraging parameters are such that there is a stable positive equilibrium, the MTE (figure 3 B) is, unsurprisingly, positively related to the equilibrium population size (figure 3 A). In the region of the parameter space where there are 3 non-zero fixed points (type III functional response, figure 1 right panel) we found extinction occurring at evolutionary time scales e.g.  $MTE > 10^{15}$ . Therefore we did not perform a detailed investigation of the model in this region of the parameter space.

Figures 4 and 5 show the direct effect of the foraging parameters on the MTE and stability coefficient (i.e., the effect when the equilibrium density is kept fixed). These show that, when the extinction state is unstable, the MTE decreases less than exponentially with handling time (figure 4), or, in the case of type III functional response, more than exponentially (figure 5). Also when the extinction state is stable, the MTE decreases less than exponentially (figure 4). We fitted exponential curves to the MTE for three different values of  $n_0$ , with type II functional response, before the transcritical bifurcation i.e. when the extinction state is unstable. We observe an increase in both the slope and the intercept with increasing carrying capacity<sup>2</sup>.

The stability of the fixed point (for details see appendix A) also has an effect on the MTE. From the lower panels of figures 4 and 5 we see that type II functional response gives rise to less stable fixed points than type III i.e., to a less negative stability coefficient. Consequently, at the same value of the stable fixed point, the MTE associated with the type II functional response is lower than the MTE associated with the type III. Moreover, while keeping the stable equilibrium fixed, the variation in MTE with handling time spans a larger interval of stability coefficient for the type III than for the type II functional response. These differences in the range of stability produce the different declines in MTE with handling time for the different functional responses (steeper for the type II figure 4 upper panel).

Overall, when we keep the stable equilibrium fixed we observe variation in the MTE by up to 5 orders of magnitude for a type II functional response and by up to 10 orders of magnitude when we have a type III functional response. This variation in MTE is shown as a function of handling time and predator abundance in figures 4 and 5 when the growth parameters are fixed and attack rate varies with handling time according to equation (10).

In figure 6 we show the effects of handling time on the QSD while keeping the stable equilibrium fixed. The width of the QSD increases with increasing handling time. Since equilibrium population size is kept constant, this increasing handling time corresponds to an increasing attack rate (expression (10)), and these both make extinction more likely (reducing the MTE). It is possible to see the influence of the unstable fixed point in the left tail of the QSD for the type II functional response (figure 6 left panels). Below the transcritical bifurcation (figure 6 A) the extinction state is unstable. After the bifurcation (figure 6 B and C) the extinction state becomes stable due to the emergence of a positive unstable fixed point, making the

<sup>2</sup>The values of the slope are fitted using a least square method and are, for different values of the fixed point:  $n_0 = 50$ , slope -133.7;  $n_0 = 60$ , slope -168.3;  $n_0 = 70$  slope -173.

left tail of the QSD increase as population size decreases towards zero. For this reason, in the parameter region after the transcritical bifurcation, the MTE of the model (4) becomes dependent on the initial population distribution. In figure 7 we show how the effect of using a delta function instead of the QSD as initial distribution can decrease the MTE by up to 2 orders of magnitude, if the initial condition is close to the (stable) extinction state (Detailed methods used to compute the MTE with different initial distributions can be found in appendix B).

Lastly, we show how allowing predator abundance to vary interacts with the effects of the foraging parameters on the MTE for both type II and type III functional responses. When predator abundance  $z$  fluctuates randomly through time the average MTE is unchanged. Consequently, the effect of foraging parameters ( $h/z$ ) on the MTE remains unchanged. Periodic variation in predator abundance can, on average, reduce or increase the MTE depending on the value of the foraging parameters (figure 8). The nature of this effect is such that the MTE decreases at low handling time and increases at high handling times. This tends to cause a shallower negative relationship between the MTE and the foraging parameters. Moreover we note that, for the type II functional response, an increase in the frequency of the periodic variation in predator abundance ( $\omega$ ) causes a larger decrease in the MTE (figure 8 A); while, for the type III functional response,  $\omega$  has no effect on the variation in MTE (figure 8 B).

#### 4. Discussion

We have shown how different choices of the foraging parameters vary the mean time to extinction by up to 10 orders of magnitude even when equilibrium population size is kept constant. Therefore, our results imply that estimates of extinction risk could be extremely inaccurate without explicitly accounting for interspecific interactions.

There is a wide literature describing experimental measures of foraging parameters (attack rate, handling time and scaling exponent) (Rall et al., 2012). These studies include predator-prey interactions among terrestrial and aquatic organisms such as protists (Hammill et al., 2010) and arthropods (Spitze, 1985; Smout et al., 2010). However similar measurements of the nature of predator-prey interactions are absent in most of the studies related to the extinction risk of individual species (Sabo et al., 2008). We found that accounting for different foraging strategies (i.e. different functional responses and different foraging parameters) can become critical when evaluating the extinction risk of a target prey species (Prowse et al., 2013).

The effects of the foraging parameters can be intuitively explained by examining the strength of population regulation at the equilibrium density i.e., the slope of the

functional response at the fixed point (Figure 2). Keeping the stable equilibrium fixed requires positive covariation between handling time and attack rate. Low handling times (equivalent to large maximum consumption rates) and low attack rates create strong regulation (line A in top left panel of Figure 2). Large handling times and attack rates result in weaker regulation (line C in top left panel of Figure 2). Strong regulation causes the population to return to the fixed point rapidly, and reduces the frequency of large fluctuations caused by demographic effects of predation. These demographic effects are independent of environmental stochasticity and become relevant for extinction risk only for small populations sizes (Lande et al., 1993; Lande and Steinar, 2004).

In (Nåsell, 2001) and (Assaf et al., 2010) an approximate expression of the quasistationary distribution and the mean time to extinction is derived for the stochastic logistic model and the SIS model of epidemics, both of these are slight simplifications of our model. Our result could be investigated more analytically using refined approximation techniques (Ovaskainen et al., 2010). The bistability emerging for high values of handling time in our study, for type III functional response, could also be investigated using approximation techniques.

Our results and main conclusion are robust to both random and periodic fluctuations of predator abundance through time. That is, the qualitative result remains; changes in the foraging parameters of the predator affect the MTE of the prey, with increases in handling time causing a decrease in MTE. Note that these results were obtained by numerical simulations, therefore they are limited to the range of parameters explored and are, thus, less general than the other analytical results presented in the paper. Understanding more generally, and in more detail, how and why variability in predator and prey growth rate affect the MTE would be a natural avenue for future research.

Another opportunity for future research is to investigate the consequences of feedbacks between prey and predator abundance by, for example, investigating a bivariate stochastic predator-prey model. Such a model could allow investigation of how the MTE depends on the strength of this feedback, which itself could result from the extent of specialism / generalism of the predator (specialist predators are likely to have stronger feedbacks Turchin (2003)). Extinction dynamics have been studied for a stochastic predator-prey model with linear interaction rates (Parker & Kamenev, 2009). It would be interesting to extend this work to include non-linear functional responses.

Further investigations could constrain analyses to regions of parameter space and combinations of foraging parameters that occur in reality. Introducing allometric rela-

tionships between foraging parameters and relating them to the growth parameters would be one way to constrain such analysis. We have shown this dependence as a function of the stable equilibrium density in equation (10). This relation can be generalized using allometric scaling relations between attack rate and handling time (Brose et al., 2006). Such an allometric scaling would require a more general formulation of the model, including predator biomass and prey biomass as other parameters.

This work has application both to studies on extinction risk and to studies on foraging theory. Most of the existing theoretical studies about complex communities do not incorporate the effects of demographic stochasticity and use deterministic measures of persistence to assess the extinction risk (Brose et al., 2004; Hofbauer et al., 2008; Dunne et al., 2009; Sahasrabudhe et al., 2011). We focused on the strong dependence of extinction times on foraging parameters in order to stress the relevance of interspecific interactions. Our approach may lead to new insights into the determinants of extinctions and can be used to increase the predictive understanding of extinction processes.

### A. Analysis of deterministic equation

We derive an adimensional formulation of (6) to simplify our subsequent analyses. We scale the number of individuals with the maximum population size  $m = n/k$ , and the characteristic time with the intrinsic birth rate  $\tau = \lambda t$ . With these rescalings, the adimensional form of equation (6) is

$$\frac{dm(\tau)}{d\tau} = m(I - m) - \frac{m^{q+1}}{a + bm^{q+1}}. \quad (14)$$

We next study the fixed points of (6) and analyze their local stability. Putting  $dm/d\tau = 0$  in equation (14), the fixed points of the system are the extinction state  $m = 0$  and the solutions of

$$bm^{q+2} - bIm^{q+1} + m^q + am - Ia = 0, \quad (15)$$

where  $I = 1 - 1/R_0$ , and  $R_0 = \lambda/\mu$  is the basic reproductive ratio, and where we introduced the following adimensional parameters:

$$a = \frac{\lambda}{\alpha k^q z}, \quad b = \lambda h \frac{k}{z}. \quad (16)$$

From the right lower panel of figure 2 we see that equation (15) has at most three real and positive solutions. Note that there will be positive solutions only when  $0 < R_0 < 1$  i.e. when  $\lambda < \mu$ .

When  $q = 0$  (type II functional response) equation (15) simplifies to

$$bm^2 + (a - bI)m + (1 - aI) = 0, \quad (17)$$

which has real solutions when  $(a + bI)^2 > 4b$ . If this condition is satisfied then the two real solutions of (17) are

$$m_{1,2} = \left( \frac{(bI - a) \pm \sqrt{(a + bI)^2 - 4b}}{2(1 - aI)} \right). \quad (18)$$

We now proceed to linear stability analysis of the fixed points of equation (14). The Jacobian of equation (14) is

$$J(m) = \frac{d}{dm} \left( \frac{dm}{d\tau} \right) = I - 2m - \frac{(q+1)am^q}{(a + bm^{q+1})^2}, \quad (19)$$

and putting  $m = 0$  in (19) implies that

- if  $q = 0$  then  $J(0) = r - \alpha z$  where  $r = \lambda - \mu$  so
  1. if  $r < \alpha z$  the extinction state is stable
  2. if  $r > \alpha z$  the extinction state is unstable
- and if  $q > 0$  the extinction state is always unstable

This stability analysis of the extinction state leads to the two extinction scenarios described in the Methods section.

### B. Mean time to Extinction

Here we present the mathematical and numerical tools needed to obtain the quasi-stationary distribution and the mean time to extinction of a general birth and death process when ultimate extinction is certain (given sufficient time). In (Nisbet and Gurney, 1982) there is a broader presentation of the methods presented hereafter. We define the process as the time evolution of a random variable  $\{X(t), t \geq 0\}$  in a finite state space  $\{0, 1, \dots, k\}$  where the origin is an absorbing barrier (Nisbet and Gurney, 1982). A convenient notation for the master equation (4) is

$$\frac{d\mathbf{p}(t)}{dt} = \mathbf{p}(t)\mathbf{A}, \quad (20)$$

where  $\mathbf{p}(t) = (p(0, t), p(1, t), \dots, p(k, t))$  is the row vector containing the state probabilities and the matrix  $\mathbf{A}$  contains the transition rates as follows:

$$\mathbf{A} = \begin{pmatrix} -G(0) & B(0) & 0 & \dots & 0 \\ D(1) & -G(1) & B(1) & \dots & 0 \\ 0 & D(2) & -G(2) & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & -G(k) \end{pmatrix}, \quad (21)$$

with  $G(n) = B(n) + D(n)$ .  $\mathbf{A}$  is a tridiagonal matrix in which all row sums equal 0. Note also that the first row is a row of zeros when using the rates (3). The solution of the master equation (4) will give the probability of having  $n$  individuals at time  $t$ ; in other words  $p(n, t) = \text{Prob}\{X(t) = n\}$ .



We now define  $T(n)$  and  $R(n)$  as

$$\begin{aligned} T(n) &= \frac{B(1)B(2)\cdots B(n-1)}{D(2)D(3)\cdots D(n)}, \\ R(n) &= \frac{B(1)B(2)\cdots B(n-1)}{D(1)D(2)\cdots D(n-1)}. \end{aligned} \quad (22)$$

Note that  $T(n) = R(n) \frac{D(1)}{D(n)}$ . Next we partition the state space of the original process into two subsets,  $\{0\}$  and  $Q = \{1, 2, \dots, k\}$ .  $Q$  is the set of transients for  $\{X(t)\}$  while  $\{0\}$  is the absorbing state for  $\{X(t)\}$ . Correspondingly we can partition the state vector  $\mathbf{p}(t)$  and the transition matrix  $\mathbf{A}$ , and obtain from equation (20)

$$\left[ \frac{dp(0,t)}{dt}; \frac{d\mathbf{p}_Q(t)}{dt} \right] = [p(0,t); \mathbf{p}_Q(t)] \begin{pmatrix} 0 & \mathbf{0} \\ \mathbf{a} & \mathbf{A}_Q \end{pmatrix}. \quad (23)$$

Here  $\mathbf{p}_Q(t)$  is the vector of probabilities in the transient states and  $\mathbf{a} = (D(1), 0, \dots, 0)^T$ . With this separation we can split the master equation (20) into:

$$\begin{aligned} dp(0,t)/dt &= \mathbf{p}_Q(t)\mathbf{a} = D(1)p(1,t), \\ d\mathbf{p}_Q(t)/dt &= \mathbf{p}_Q(t)\mathbf{A}_Q. \end{aligned} \quad (24)$$

Before absorption (extinction) the process takes values in the set of the transients. As in equation (7) we define the conditional probability  $p_c(n,t) = P\{X(t) = n | X(t) > 0\}$  of having  $n$  individuals at time  $t$  knowing absorption (extinction) has not occurred and, using equations (24), this can be expressed as

$$\mathbf{p}_c(t) = \frac{\mathbf{p}(t)}{1 - p(0,t)} = \frac{\mathbf{p}_Q(t)}{1 - p(0,t)}. \quad (25)$$

Differentiating equation (25) and using the master equation (4) and equations (24) we obtain an equation for  $\mathbf{p}_c(t)$ :

$$\begin{aligned} \frac{d\mathbf{p}_c(t)}{dt} &= \frac{d\mathbf{p}_Q}{dt} \left( \frac{1}{1 - p(0,t)} \right) + \frac{\mathbf{p}_Q(t)}{(1 - p(0,t))^2} \frac{dp(0,t)}{dt} \\ &= \mathbf{p}_c(t)\mathbf{A}_Q + D(1)p_c(1,t)\mathbf{p}_c(t). \end{aligned} \quad (26)$$

Setting the the right-hand side of expression (26) equal to zero we obtain an equation for the quasi-stationary distribution  $\boldsymbol{\pi} = (\pi(1), \pi(2), \dots, \pi(k))$ , defined as the distribution of the transient states conditioned on the fact that there has not yet been extinction:

$$\boldsymbol{\pi}\mathbf{A}_Q = -D(1)\boldsymbol{\pi}(1)\boldsymbol{\pi}. \quad (27)$$

In other words the quasistationary distribution  $\boldsymbol{\pi}$  is the left eigenvector of  $\mathbf{A}_Q$  with eigenvalue  $-D(1)\pi(1)$ .

It can be shown that  $\pi(n)$  satisfies the recursive formula:

$$\pi(n) = T(n) \sum_{i=1}^n \frac{(1 - \sum_{j=1}^{i-1} \pi(j))}{R(i)} \pi(1). \quad (28)$$

Once  $\pi(1)$  is known then  $\pi(2), \pi(3), \dots, \pi(n)$  can be determined iteratively. But  $\pi(1)$  can only be obtained by knowing all other elements to  $\sum_n \pi(n) = 1$ . For this reason the analytic determination of  $\boldsymbol{\pi}$  is limited to birth death processes with linear transition rates and this is not our case. However there is an iterative method that can be used to derive numerical approximations for the quasistationary distribution of our process:

- Start with an initial guess for  $\pi(1)$ .
- Obtain all the  $\pi(n)$  using the (28) and compute  $S = \sum_n \pi(n)$ .
- Start the iteration again with  $\pi^I(1) = \pi(1)/S$  and obtain  $\pi^I(n)$ .
- Repeat the process until  $\|\pi^{K+1}(n) - \pi^K(n)\| < \delta$ . The value  $\delta$  gives the precision of the algorithm.

Figure 9 shows example results from implementing this procedure to derive the QSD of the birth-death process (4) with a type II functional response.

The time to extinction  $\tau^3$  is a random variable that depends on the initial distribution of the process (Nåsell, 2001). We call  $\tau_Q$  the time to extinction of the birth-death process when the quasi stationary distribution  $\boldsymbol{\pi}$  is set as an initial condition, and  $\tau_n$  is the time to extinction when the initial condition is  $X(0) = n$  i.e., when  $p(n, 0) = 1$ . If absorption has occurred at time  $t$  then the events  $\{\tau < t\}$  and  $\{X(t) = 0\}$  are identical:

$$P\{\tau < t\} = P\{X(t) = 0\} = p(0,t). \quad (29)$$

Once the quasistationary distribution is known then the MTE<sup>4</sup> is given by expression (9).

The explicit expression of the time to extinction with an arbitrary initial condition is more difficult to obtain. It is a standard result for birth death processes theory (Nisbet and Gurney, 1982) that the expectation of  $\tau_n$  can be determined explicitly when  $X(0) = n$ :

$$E(\tau_n) = \frac{1}{D(1)} \sum_{i=1}^n \frac{1}{R(i)} \sum_{j=i}^k T(j). \quad (30)$$

Moreover the expected time to extinction for an arbitrary initial distribution  $\{p(n, 0)\}$  can be derived from (30):

$$E(\tau) = \frac{1}{D(1)} \sum_{j=1}^k T(j) \sum_{i=1}^j \frac{1}{R(i)} \sum_{n=i}^k p(n, 0), \quad (31)$$

with the assumption that the initial distribution is supported on the set of the transient states.

<sup>3</sup>this  $\tau$  is different from the adimensional time used in appendix A

<sup>4</sup>note that with our notation  $MTE = E(\tau_Q)$ .

# Acknowledgments

GMP would like to thank Antonio Scala, Rich Williams and professor Stanislav Molchanov for invaluable support and discussions, and two anonymous reviewers for helpful comments. The project is funded by Microsoft Research and the University of Zurich.

- Lande, R., E. Steinar and B. E. Sæther. "Stochastic population dynamics in ecology and conservation", Oxford series in Ecology and Evolution. (2004)
- Bascompte, J., and R. V. Solé. "Rethinking complexity: modelling spatiotemporal dynamics in ecology." *Trends in Ecology & Evolution* **10**, 3616. (1995)
- McCann, K. S. "The diversity-stability debate." *Nature* **405**, 228-33. (2000)
- Allesina, S., and S. Tang. "Stability criteria for complex ecosystems." *Nature*. (2012)
- Witting, L., J. Tomiuk, and V. Loeschcke. "Modelling the optimal conservation of interacting species." *Ecological Modelling*, **125** 123144. (2000)
- Liebold, A., and J. Bascompte. "The Allee effect, stochastic dynamics and the eradication of alien species." *Ecology Letters*, **84**, 468140. (2003)
- Lande, R. "Risks of population extinction from demographic and environmental stochasticity and random catastrophes." *The American Naturalist* **142**, 911-927. (1993)
- Foley, P. "Predicting extinction times from environmental stochasticity and carrying capacity." *Conservation Biology* **8**, 124-137. (1994)
- Purvis, A., J. L. Gittleman, G. Cowlshaw, and G. M. Mace. "Predicting extinction risk in declining species." *Proceedings of the Royal Society B: Biological Sciences* **267**, 1947-52. (2000)
- Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. "Predictive accuracy of population viability analysis in conservation biology." *Nature* **404**, 385-7. (2000)
- "Population viability analysis", edited by S. R. Beissinger and D. R. McCullough. University of Chicago Press, Chicago. (2002)
- Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart. "Quantification of extinction risk: IUCN's system for classifying threatened species." *Conservation Biology* **22**, 1424-42. (2008)
- Sabo, J. L., and L. R. Gerber. "Predicting extinction risk in spite of predator-prey oscillations." *Ecological Applications* **17**, 1543-1554. (2007)
- Sabo, J. L. "Population viability and species interactions: Life outside the single-species vacuum." *Biological Conservation* **141**, 276-286. (2008)
- Holling, C. S. "Some characteristic of simple types of predation and parasitism." *The Canadian Entomologist* **XCI**, 385-398. (1959)
- Real, L. A. "The kinetics of functional response." *The American Naturalist* **111**, 289-300. (1977)
- Abrams, P. A., and L. R. Ginzburg. "The nature of predation: prey dependent, ratio dependent or neither?" *Trends in Ecology & Evolution* **15**, 337-341. (2000)
- Jeschke, J. M., M. Kopp, and R. Tollrian. "Predator functional responses: discriminating between handling and digesting prey." *Ecological Monographs* **72**, 95-112. (2002)
- Holling, C. S. "The functional response of predators to prey density." *Memoirs of the Entomological Society of Canada* **45**, 1-60. (1965)
- Jeschke, J. M., M. Kopp, and R. Tollrian. "Consumer-food systems: why type I functional responses are exclusive to filter feeders." *Biological Reviews* **79**, 337349. (2004)
- Turchin, P. "Complex population dynamics." Princeton University Press. (2003)
- Smout, S., C. Asseburg, J. Matthiopoulos, C. Fernández, S. Redpath, S. Thirgood, and J. Harwood. "The functional response of a generalist predator." *PloS one* **5**, e10761. (2010)
- Vucic-Pestic, O., K. Birkhofer, B. C. Rall, S. Scheu, and U. Brose. "Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction." *Pedobiologia* **53**, 307-312. (2010)
- May, R. M. "Stability and complexity in model ecosystems." Princeton University Press. (2001)
- Drossel, B., A. J. McKane, and C. Quince. "The impact of nonlinear functional responses on the long-term evolution of food web structure." *Journal of Theoretical Biology* **229**, 539-48. (2004)
- McKane, A. J., and T. J. Newman. "Stochastic models in population biology and their deterministic analogs." *Physical Review E* **70**, 1-19. (2004)
- Ebenman, B., R. Law, and C. Borrvall. "Community viability analysis: the response of ecological communities to species loss." *Ecology* **85**, 25912600. (2004)
- Powell, C. R., and R. Boland. "The effects of stochastic population dynamics on food web structure." *Journal of Theoretical Biology*, **257**, 170-80. (2009)
- Black, A. J., and A. J. McKane. "Stochastic formulation of ecological models and their applications." *Trends in Ecology & Evolution*, 1-9. (March 2012).
- McKane, A. J., and T. J. Newman. "Predator-Prey Cycles from Resonant Amplification of Demographic Stochasticity." *Physical Review Letters* **94**, 1-4. (2005)
- Parker, M., and A. Kamenev. "Extinction in the Lotka-Volterra model." *Physical Review E* **80**. (2009)
- Kramer, A. M., and J. M. Drake. "Experimental demonstration of population extinction due to a predator-driven Allee effect." *The Journal of Animal Ecology* **79**, 6339. (2010)
- Nisbet, R. M. and W. C. S. Gurney. "Modelling fluctuating population". The Blackburn Press. (1982)
- Näsell, I. "Extinction and quasi-stationarity in the Verhulst logistic model." *Journal of Theoretical Biology* **211**, 11-27. (2001)
- Hammill, E., O. L. Petchey, and B. R. Anholt. "Predator functional response changed by induced defenses in prey." *The American Naturalist* **176**, 723-731. (2010)
- Hanski, I., L. Hansson, and H. Henttonen. "Specialist predators, generalist predators, and the microtine rodent cycle." *Journal of Animal Ecology* **60**, 353367. (1991)
- Williams, R. J., and N. D. Martinez. "Stabilization of chaotic and non-permanent food-web dynamics." *The European Physical Journal B* **38**, 297-303. (2004)
- Gardinier, C. "Stochastic Methods: A Handbook for the Natural and Social Sciences", Springer. (2009)
- Assaf, M., and B. Meerson. "Extinction of metastable stochastic populations." *Physical Review E* **81**, 1-18. (2010).
- Bartlett M. S.. "Stochastic Population Models in Ecology and Epidemiology". Methuen, London. (1960)
- Gillespie, D. T. "Exact stochastic simulation of coupled chemical reactions." *The Journal of Physical Chemistry*, **81**, 23402361. (1977)
- Taylor, R. A., J. A. Sherratt, and A. White. "Seasonal forcing and multi-year cycles in interacting populations: lessons from a predator-prey model." *Journal of Mathematical Biology*. (2013).
- Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, O. L. Petchey. "Universal temperature and body mass scaling of feeding rates" *Philosophical Transactions of the Royal society* **367**, 2923-34. (2012)
- Spitze, K. "Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia Pulex*." *Ecology* **66**, 938-949. (1985)
- Prowse T. A. A., C. N. Johnson, R. C. Lacy, C. J. A. Bradshaw, J. P. Pollak, M. J. Watts, and B. W. Brook. "No need for disease: testing extinction hypotheses for the thylacine using multi-species metamodels." *Journal of Animal Ecology*, **82**, 355364. (2013)
- Ovaskainen, O., and B. Meerson. "Stochastic models of population extinction." *Trends in Ecology & Evolution* **25**, 643-652. (2010)
- Brose, U., R. J. Williams, and N. D. Martinez. "Allometric scaling enhances stability in complex food webs." *Ecology Letters* **9**, 1228-36. (2006)
- Brose, U., A. Ostling, K. Harrison, and N. D. Martinez. 2004. "Unified spatial scaling of species and their trophic interactions." *Nature*

- ture **428**, 167171. (2004)
- Hofbauer, J., R. Kon, and Y. Saito. "Qualitative permanence of Lotka-Volterra equations." *Journal of Mathematical Biology* **57**, 863-81. (2008)
- Dunne, J. A., and R. J. Williams. "Cascading extinctions and community collapse in model food webs." *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1711-23. (2009)
- Sahasrabudhe, S., and A. E. Motter. "Rescuing ecosystems from extinction cascades through compensatory perturbations." *Nature Communications* **170**, 1-21. (2011)

Accepted manuscript



Figure 1: Regions in parameter space where the model (6) has 0, 1, 2 and 3 non-zero fixed points and their associated stability. The axes are handling time divided by predator abundance  $h/z$  and attack rate multiplied by predator abundance  $\alpha_p = z\alpha$ . The growth parameters are fixed as  $\lambda = 1.5 d^{-1}$ ;  $\mu = 0.5 d^{-1}$  and  $k = 150$ .



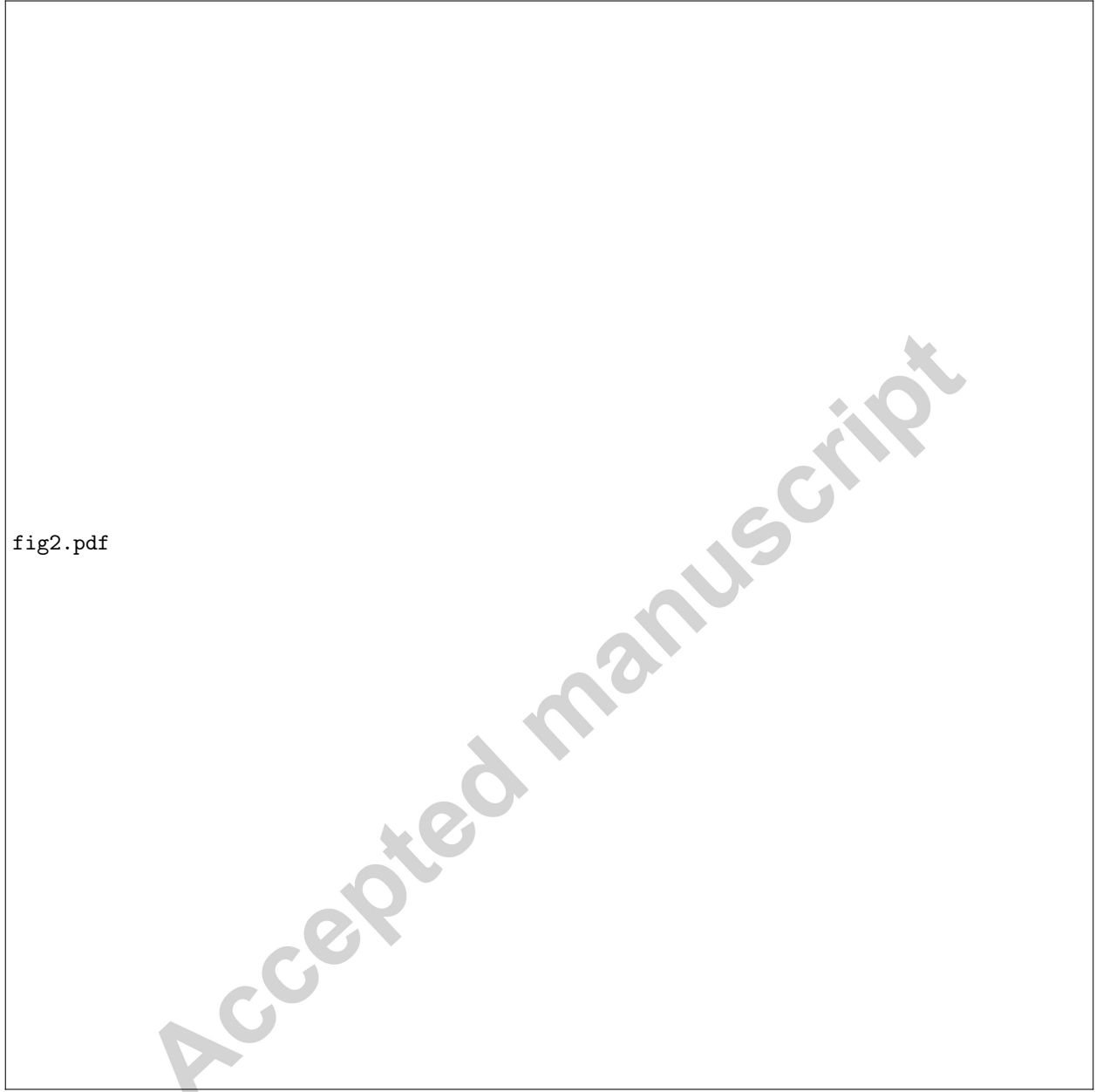


Figure 2: Prey population mortality due to predation (left panels) and per capita mortality due to predation (right panels) following a type II (upper panels) and a type III (lower panels) functional response. On the left plots solid lines are the population functional responses. On the right plots solid lines are the per capita functional responses while the dashed line is the per capita growth curve ( $\lambda = 1.5 d^{-1}$ ;  $\mu = 0.5 d^{-1}$  and  $k = 150$ ). The foraging parameters are for the type II functional response A:  $h/z = 0.001 d$ ;  $\alpha z = 0.5 d^{-1}$ . B:  $h/z = 0.02 d$ ;  $\alpha z = 1 d^{-1}$  at the transcritical bifurcation. C:  $h/z = 0.03 d$ ;  $\alpha z = 2.05 d^{-1}$ . And for the type III functional response D:  $h/z = 0.001 d$ ;  $\alpha z = 0.01 d^{-1}$ . E:  $h/z = 0.02 d$ ;  $\alpha z = 0.02 d^{-1}$ . F:  $h/z = 0.18 d$ ;  $\alpha z = 0.037 d^{-1}$ . Note that with this particular choice of foraging parameters the value of the fixed point is fixed at  $n_0 = 50$ .



Figure 3: Abundance  $n_0$  at the stable fixed point predicted by equation (6) (A) and the log of the mean time to extinction (MTE) (B) of the birth and death process (3) using the quasistationary distribution as initial condition as a function of handling time and attack rate for type II functional response. The growth parameters are as specified in the legend of figure 1.

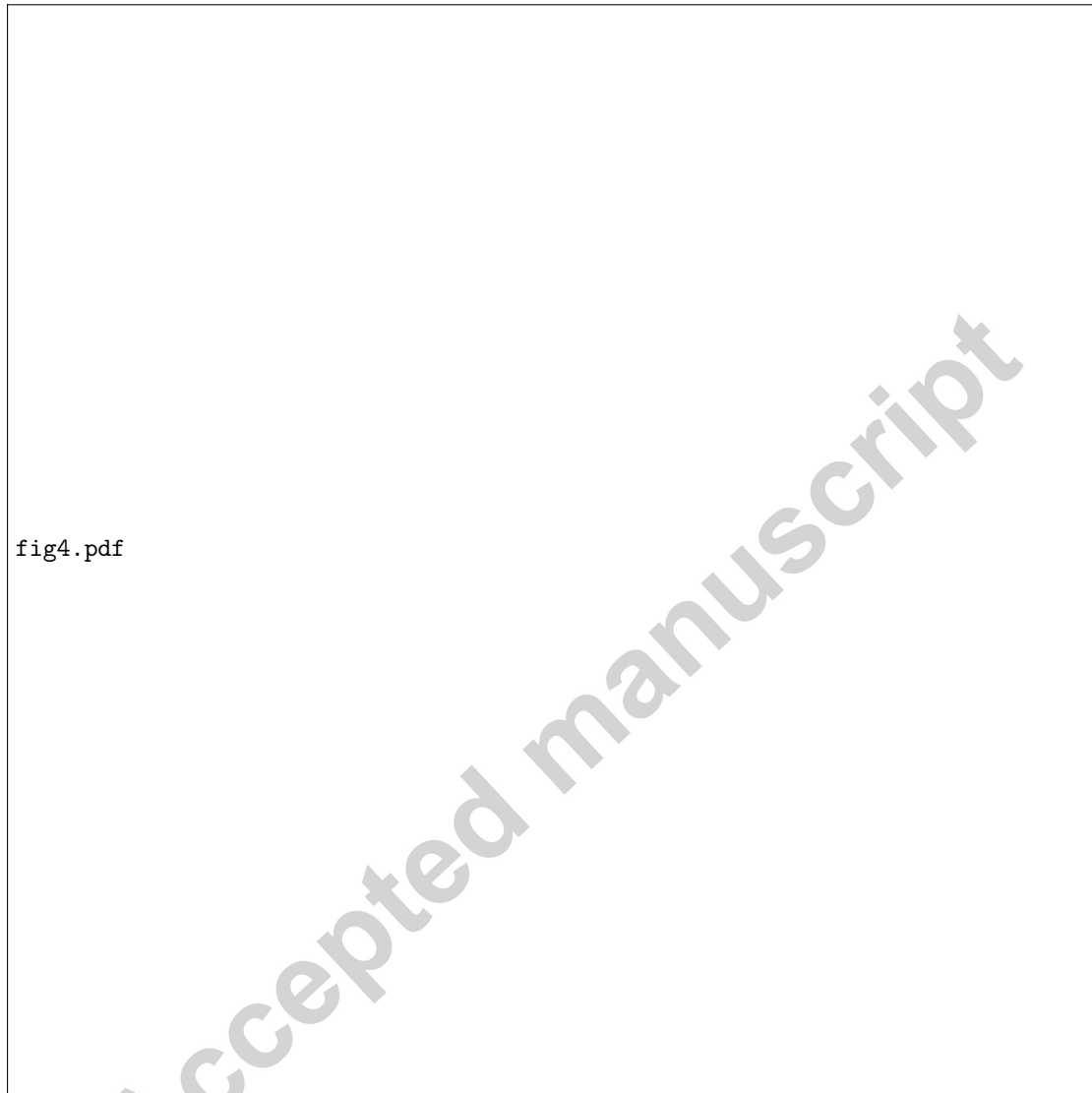


Figure 4: Logarithm of the mean time to extinction (MTE) (when the quasistationary distribution is set as initial condition of equation (4)) as a function of handling time (A) and of the stability coefficient (B), for different values of the stable fixed point  $n_0$ , for a type II functional response. The dashed line divides the parameter space into two regions. A region associated with an unstable extinction state (above and left) and a region associated with a stable extinction state (below and right). The curves are drawn for all values of handling time which keep the stable equilibrium density  $n_0$  fixed and the corresponding attack rate (10) finite i.e., for  $h < \min(h_1, h_0)$ . The values of  $h_1$  and  $h_0$  are obtained from expressions (11) and (12). We used expression (9) to obtain the MTE. The stability coefficient is the real part of the Jacobian computed in  $n_0$  (see appendix A). The growth parameters are as specified in the legend of figure 1.



Figure 5: Logarithm of the mean time to extinction (MTE) as a function of handling time ( $C$ ) and of the stability coefficient ( $D$ ), for different values of the stable fixed point  $n_0$ , for type III functional response ( $q = 1$ ). We used expression (9) to obtain the MTE. The growth parameters are as specified in the legend of figure 1.





Figure 6: Quasistationary distribution of the model (4) when keeping the stable equilibrium fixed at  $n_0 = 70$  (A, D),  $n_0 = 60$  (B, E),  $n_0 = 50$  (C, F) for type II (left panels) and type III (right panels) functional response. The gray scale represents increasing handling time over fixed predator abundance.



Figure 7: Relative difference between the logarithm of the MTE obtained when the QSD is set as initial distribution ( $\tau_Q$ ) and the logarithm of the MTE when  $\delta(n)$  is chosen as initial distribution ( $\tau_n$ ), as a function of handling time over predator abundance, for type II functional response when the equilibrium density is kept fixed at  $n_0 = 50$ .



Figure 8: Relative difference between the logarithm of the MTE obtained numerically with a predator seasonality given by expression (13) ( $\tau_z$ ) and the logarithm of the MTE when the predator abundance is fixed ( $\tau_Q$ ), as a function of handling time over predator abundance. Simulations are done for type II (A) and type III (B) functional response with the foraging parameters of the model with fixed predator abundance when the equilibrium prey population size is kept fixed at  $n_0 = 50$  and the QSD is set as initial condition (100 replicates).



Figure 9: Quasistationary distribution (QSD) of the model (4) as a function of handling time over predator abundance for type II functional response at fixed attack rate per predator abundance  $\alpha z = 1.5d^{-1}$ . The continuous line represents the stable fixed point while the dashed line represents the unstable fixed point of the model. The other parameters are as specified in the legend of figure 1