The hydra effect in predator–prey models

Michael Sieber · Frank M. Hilker

Abstract   The seemingly paradoxical increase of a species population size in response to an increase in its mortality rate has been observed in several continuous-time and discrete-time models. This phenomenon has been termed the "hydra effect". In light of the fact that there is almost no empirical evidence yet for hydra effects in natural and laboratory populations, we address the question whether the examples that have been put forward are exceptions, or whether hydra effects are in fact a common feature of a wide range of models. We first propose a rigorous definition of the hydra effect in population models. Our results show that hydra effects typically occur in the well-known Gause-type models whenever the system dynamics are cyclic. We discuss the apparent discrepancy between the lack of hydra effects in natural populations and their occurrence in this standard class of predator–prey models.

Keywords   Consumer–resource models · Gause-type model · Population cycles · Allee effect · Mean population density · Population extinction

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1 Introduction

In a recent review Abrams (2009) discusses the counterintuitive increase of a species population size in response to an increase in its mortality rate. This phenomenon has

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been termed "hydra effect" by Abrams and Matsuda (2005), after the nine-headed beast from Greek mythology that would grow two more heads for each that was cut off. Effects that qualify as hydra effects had already been described by Ricker (1954) and, without necessarily calling them hydra effects, they have been shown to occur in discrete-time (Sinha and Parthasarathy 1996; Schreiber 2003; Hilker and Westerhoff 2006; Seno 2008; Zipkin et al. 2009; Liz 2010; Dattani et al. 2011) and continuous-time models (Abrams et al. 2003; Matsuda and Abrams 2004) as well as in delay differential equations (Terry and Gourley 2010); see also Abrams (2009) for more references. As has been pointed out by Abrams (2009), empirical evidence for hydra effects is rare and this poses the question whether this is due to a lack of appropriate observations or due to shortcomings of the underlying theoretical models. This question is complicated by the fact that analytical results concerning the hydra effect are also rare and mainly heuristic explanations have been given to define and explain hydra effects in ecological terms. Abrams (2009) names, for example, altered population cycles, consumer mortality leading to more prudent resource exploitation and temporal separation of mortality and density-dependent processes as possible mechanisms leading to hydra effects. These explanations are illustrated by numerical simulations, focusing on a few well-known models. While this already shows that hydra effects are not an uncommon phenomenon in ecological models, we propose to rigorously define the term "hydra effect". This allows to formalize the understanding of the term and to derive analytical results. This is the purpose of this paper, where we will address the phenomenon of the hydra effect in a series of continuous-time models.

Our main analytical results are (a) that hydra effects are typical for Gause-type predator–prey models and (b) that they occur whenever an unstable coexistence equilibrium exists. Our results also imply that increasing predator mean densities occur necessarily right before a further increase in predator mortality may drive the population to extinction, thereby giving a false impression of the healthiness and sustainability of the population.

The paper is organized as follows. The next section introduces a general population model and some basic notation. The third section recalls some well-known results regarding mean values of solutions to differential equations and it gives a rigorous definition of the hydra effect. The fourth section contains the main result that hydra effects are a typical feature of Gause-type predator–prey models. This is illustrated by a suite of some of the most commonly used examples. The fifth section discusses hydra effects in a three-species model. Finally, the last section discusses the implications of the results and identifies avenues for future research.

2 Population models and mortality rates

We adopt the basic assumption that the population dynamics of an ecological community of n species can be modeled by the parameter-dependent differential equation

$$\dot{Y} = f(Y, m), \tag{1}$$

with $f : D \subseteq \mathbf{R}^n \to \mathbf{R}^n$ and $\dot{Y} = \frac{dY}{dt}$. The domain D of the vectorfield f is assumed to be an open subset of $\mathbf{R}^n$ and will be referred to as the phase space of system (1).

The biologically reasonable subset of the phase space is $D_{\geq 0} = D \cap \mathbf{R}_{\geq 0}^n$, where $\mathbf{R}_{\geq 0}$ denotes the non-negative real numbers. Correspondingly, the strictly positive real numbers are denoted $\mathbf{R}_{>0}$. A solution Y is given by a real-valued function $Y(t, \xi, m)$ satisfying (1), which depends on the initial condition $\xi \in D$ and the parameter m. The components $Y = (y_1, \ldots, y_n)$ of a solution correspond to the population densities of the n respective species, and the ith component of $f = (f_1, \ldots, f_n)$ describes the growth and interaction of the ith species. We make the following assumptions concerning the vectorfield f. First, f is assumed to be sufficiently smooth, being at least C^1 in Y and m on the open set $D \times \mathbf{R}_{>0}$. Second, since (1) is supposed to describe the population dynamics of biological species, we require that all components of $Y(t, \xi)$ with $\xi \in D_{\geq 0}$ remain non-negative for all times. Third, we assume that all solutions eventually enter and remain in a compact absorbing set $K \subset D_{\geq 0}$, e.g. the population densities of all species are ultimately bounded. These assumptions ensure the uniqueness and existence of solutions starting in $D_{\geq 0}$ for all forward times. Note that throughout this paper by an equilibrium or stationary solution we mean a point satisfying $f(\xi) = 0$ and by a cycle we mean a periodic solution with $Y(t) = Y(t+T)$ for all t and some period $T > 0$ so that $Y(t) \neq Y(t + \tau)$ for $0 < \tau < T$.

While we make no assumptions about the particular form of the functions f_i, for the sake of clarity we deliberately restrict our analysis to systems where the growth and interaction rate of at least one species can be written as

$$f_i(Y, m) = g_i(Y) - my_i,$$

where g_i and f_j, $j \neq i$ do not depend on m. The parameter $m > 0$ will be denoted as per-capita *mortality rate* of species i. Note that mortality rate in the sense of this assumption may not only include the natural mortality rate of a species, but also processes such as harvesting, culling or other forms of removal.

For many ecological systems, it is important to understand how the population size of a focal species responds to an increase in its mortality rate. When the population dynamics approach an equilibrium, this amounts to solving an algebraic problem. However, when there are nonequilibrium dynamics, the problem becomes much more difficult since one has to assess the mean population size, where ideally the average is taken over a long time interval to avoid the influence of transient effects.

3 Definition of mean population density and the hydra effect

As indicated in the previous section, we are often interested in the long-term behavior of solutions to Eq. (1) and in particular the mean abundance of a population. The following definition of the average size of a population is the one implicitly used in all previous studies that have addressed the hydra effect.

Definition 1 Let $\phi : M \times \mathbf{R}_{>0} \to \mathbf{R}^n$ be the *mean value map*

$$\phi(\xi, m) = \lim_{t \to \infty} \frac{1}{t} \int_0^t Y(s, \xi, m) \, ds,$$

where $M \subseteq D$ is the subset of initial conditions for which the limit on the right-hand side exists. The map assigns to a point $\xi \in M$ and a mortality rate the *asymptotic mean value* of the parameter-dependent solution $Y(t, \xi, m)$ through this point. Integration of the solution Y is componentwise as usual and $\phi_i(\xi, m)$ is the asymptotic mean value of the ith species. If either the initial condition or the mortality rate is fixed, we will frequently simplify notation to $\phi(m)$ or $\phi(\xi)$, respectively.

Note that in general M will be a proper subset of the phase space D. For example, consider a model of nontransitive competition, in which three species coexist via cyclic domination—an ecological variant of the rock-scissors-paper game (May and Leonard 1975). For this model Gaunersdorfer (1992) has shown that asymptotic mean values do not exist for large regions of the phase space. This result is related to the formation of a heteroclinic cycle connecting three equilibrium points and the exponentially lengthening periods of time a solution approaching this cycle spends in the vicinity of each of these equilibria.

Nevertheless, the existence of the asymptotic mean value is ensured in the situations we are mainly concerned with. Therefore, let us first recall the notion of the stable set of a solution.

Definition 2 The *stable set* $A(Y)$ of a solution $Y(t, \xi)$ is the set of all points which get attracted to Y for large times:

$$A(Y) = \{\eta \in D | \exists\, t_0 \geq 0 : Y(t_0, \xi) = \xi_0 \text{ and } \lim_{t \to \infty} \|X(t, \eta) - Y(t, \xi_0)\| = 0\}.$$

Since we are only interested in positive solutions, a solution $Y(t, \xi)$ is called *globally stable* if it attracts all strictly positive initial conditions.

The following result now implies that the mean value map, if it is well defined, is in fact constant on the stable set of a solution.

Proposition 1 Let $Y(t, \xi)$ be a solution of (1) and let $\phi(\xi)$ exist. Then $\phi(\eta) = \phi(\xi)$ for all $\eta \in A(Y)$.

Proof Let $\phi(\xi) = L$. We first observe that this mean value is of course the same for all points on the solution $Y(t, \xi)$. Namely, with $Y(t_0, \xi) = \xi_0$ for some $t_0 > 0$ a reparametrization of time yields

$$\phi(\xi) = \lim_{t \to \infty} \frac{1}{t} \int_0^t Y(s, \xi)\, \mathrm{d}s = \lim_{t \to \infty} \frac{1}{t} \left[\int_0^{t_0} Y(s, \xi)\, \mathrm{d}s + \int_{t_0}^t Y(s, \xi)\, \mathrm{d}s \right]$$

$$= \lim_{t \to \infty} \frac{1}{t} \int_{t_0}^t Y(s, \xi)\, \mathrm{d}s = \lim_{t \to \infty} \frac{1}{t} \int_0^t Y(s, \xi_0)\, \mathrm{d}s = \phi(\xi_0).$$

Now assume that a different solution $X(t, \eta)$ with $\eta \in A(Y)$ exists. Then there is a ξ_0 so that $\lim_{t \to \infty} \|X(t, \eta) - Y(t, \xi_0)\| = 0$, which implies $\lim_{t \to \infty} [x_i(t, \eta) - y_i(t, \xi_0)] = 0$

for each coordinate $i = 1, \ldots, n$. Now define $F_i(t) = \int_0^t [x_i(s, \eta) - y_i(s, \xi_0)] \, ds$ and $G(t) = t$. Then $\lim_{t \to \infty} G(t) = \infty$ and using L'Hôpital's rule we obtain:

$$\lim_{t \to \infty} \frac{F_i(t)}{G(t)} = \lim_{t \to \infty} \frac{F_i'(t)}{G'(t)} = \lim_{t \to \infty} [x_i(t, \eta) - y_i(t, \xi_0)] = 0.$$

Now, since $\phi_i(\xi_0) = \lim_{t \to \infty} \frac{1}{t} \int_0^t y_i(s, \xi_0) \, ds = L_i$ and

$$\lim_{t \to \infty} \frac{F_i(t)}{G(t)} = \lim_{t \to \infty} \left[\frac{1}{t} \int_0^t x_i(s, \eta) \, ds - \frac{1}{t} \int_0^t y_i(s, \xi_0) \, ds \right] = 0,$$

this implies $\phi_i(\eta) = \phi_i(\xi_0) = L_i$.

Before proceeding, let us turn to two important special cases in which we need not consider infinite time intervals to obtain the asymptotic mean value. In the case of a stationary solution the mean value is of course the equilibrium value itself and thus equilibria of (1) are fixed points of the mean value map. And for periodic solutions the asymptotic mean value can obviously be obtained from a single period. This is summarized in the following proposition.

Proposition 2 *Let $Y(t, \xi)$ be a solution of* (1).

  (i)   *If ξ is an equilibrium, then $\phi(\xi) = \xi$.*
  (ii)   *If Y is a cycle with period T, then $\phi(\xi) = \frac{1}{T} \int_0^T Y(s, \xi) \, ds$.*

During the following analysis we will be mainly concerned with these two special cases for which asymptotic mean values surely exist. However, in a more general setting ergodic theory tells us when these long time averages are well defined (Eckmann and Ruelle 1985).

Now that we have recalled some basic properties of the mean value map $\phi(\xi, m)$, we can study how the mean population density of a species changes with respect to its mortality rate. Intuitively, in an ecological scenario one would expect a species mean population density to decrease if its mortality increases for some reason. The apparently paradoxical situation, where the mean population density of a species increases in response to an increasing mortality rate, has been termed the hydra effect.

Definition 3 Species i is said to experience a *hydra effect*, if there exist an initial condition $\xi \in D_{\geq 0}$ and mortality rates $m_1 < m_2$ so that $\phi_i(\xi, m_1) < \phi_i(\xi, m_2)$. The hydra effect is *smooth* if $\phi_i(\xi, m)$ is continuous on $[m_1, m_2]$, otherwise it is *non-smooth*.

Note that this definition distinguishes two qualitatively different types of hydra effects. Smooth hydra effects occur when an attractor of system (1) smoothly changes its position or shape in phase space in response to a change in the mortality rate. The simplest example of a smooth hydra effect would be given by a stable equilibrium $E^* = (y_1^*, \ldots, y_n^*)$ of system (1), for which $\partial y_i^* / \partial m > 0$ holds with m being the mortality rate of the ith species. This form of a smooth hydra effect may occur in stage-structured models which introduce a temporal separation between mortality

and density-dependent growth, a scenario discussed by Abrams (2009) for a model describing the dynamics of juvenile and mature subpopulations. The most prominent examples of hydra effects are however associated with smooth changes in the amplitude of population cycles (Abrams 2009), which will be discussed in Sect. 4.1 for Gause-type predator–prey models.

On the other hand, non-smooth hydra effects are characterized by a discontinuous change in a species mean population density. There are essentially two scenarios, which can lead to non-smooth hydra effects. The first scenario arises when attractors suddenly appear or vanish due to global bifurcations. A striking form of a non-smooth hydra effect due to this scenario may occur when strictly positive attracting solutions to Eq. (1) do not exist for low mortality rates, but emerge suddenly via a global bifurcation. This is a typical scenario when the growth of a prey species is subject to a strong Allee effect, cf. Sect. 4.3. The second scenario which may lead to non-smooth hydra effects is associated with multiple coexisting attractors, where the boundaries of the respective basins of attraction shift in response to changes in a species mortality rate. The long-term behavior of a solution starting at a particular initial condition ξ may then undergo a discontinuous change when ξ switches from one basin of attraction to another. Non-smooth hydra effects due to this second scenario in a two-stage model by Schreiber and Rudolf (2008) have been referred to as "very large magnitude hydra effects" by Abrams (2009). Although non-smooth hydra effects may appear as especially striking since the associated jump in species mean density occurs suddenly and without warning, this term is somewhat misleading since non-smooth hydra effects need not be of large magnitude at all, cf. Sect. 5.

4 The hydra effect in models of purely prey-dependent predator growth

An important class of predator–prey equations is obtained by assuming that the per-capita growth rate of each predator does not depend on its own density. These systems will be called *pure predator systems* in the following, in analogy to "pure resource–consumer systems" where the per-capita growth rates of all species are independent of their own respective density (Turchin 2003, p. 34). In the following we will consider mainly two- or three-dimensional systems and we write $Y = (x, y, z)$ for the components of respective solutions. Consequently, ϕ_x denotes the asymptotic mean density of species x.

4.1 Gause-type models

In this section we will show that the predator typically experiences a hydra effect in a class of standard predator–prey models. We obtain this class of models by assuming that prey per-capita growth g and the predation term ρ are functions only of the prey density. These assumptions lead to the general model (Gause 1934)

$$\dot{x} = g(x)x - \rho(x)y, \tag{2}$$
$$\dot{y} = \varepsilon\rho(x)y - my, \tag{3}$$

for the prey density x and the predator density y. Here, $\varepsilon\rho$ denotes the numerical response of the predator, which accounts for the limited conversion efficiency ε. The parameter m is the predator's mortality rate. These general equations have been used over decades as a cornerstone of theoretical predator–prey ecology (May 1976; Yodzis 1989; Turchin 2003). A significant feature of Eqs. (2)–(3) is that predator growth is purely prey dependent. In ecological terms this means that predator individuals are assumed not to interact with each other, but only indirectly through the consumption of the prey. From now on we will consider system (2)–(3) with the following assumptions (A)–(C).

(A) There exists $0 < K$ such that $(x - K)g(x) < 0$ for $x \geq 0$, $x \neq K$.
(B) $\rho(0) = 0$ and $\rho'(x) > 0$ for $x > 0$.

Assumption (A) basically introduces a self-limitation of the prey population, with positive per-capita prey growth for all prey densities below a certain carrying capacity K and negative per-capita growth if prey density exceeds this value. This excludes a strong Allee effect, which we are going to study in Sect. 4.3. Assumption (B) states that predator consumption is a strictly increasing function of prey density. This includes the linear functional response of Lotka–Volterra type as well as functional responses with a saturation effect (e.g., Holling-type II and III), but not type IV functional responses. Both assumptions (A) and (B) are consistent with standard predator–prey theory and they have clear biological interpretations. Note that under assumptions (A) and (B) all solutions of system (2)–(3) starting in the positive quadrant are ultimately bounded (Bauer 1979) and eventually remain in a compact subset of the phase space. As an important consequence of (A) and (B) we have that whenever $x^* > 0$ exists so that $\varepsilon\rho(x^*) = m$, it is unique. With the non-trivial part of the prey nullcline

$$\nu(x) = x \frac{g(x)}{\rho(x)},$$

this gives rise to the unique positive equilibrium $E^* = (x^*, \nu(x^*))$ of Eqs. (2)–(3), which exists for $0 < x^* < K$. The function ν will simply be denoted the *prey nullcline* from now on, neglecting the trivial part $x = 0$.

The hydra effect is defined in terms of the mortality rate m, and due to the purely prey-dependent predator y there is a close connection between m and the location of the equilibrium E^*. The predation term ρ is a strictly increasing function of x, and thus for fixed ε the equation $\dot{y} = 0$ implies a strictly increasing map $x^*(m) = \rho^{-1}(m/\varepsilon)$, mapping a mortality rate to a prey density. Here, ρ^{-1} denotes the inverse of ρ. Setting $\nu(m) = \nu \circ x^* = \nu(x^*(m))$, we can consider the set of equilibria $E^*(m) = (x^*(m), \nu(m))$ as a smooth curve in phase space parameterized by the mortality rate m. The equilibrium $E^*(m)$ exists for all $m \in\,]0, m_+[$, where $x^*(m_+) = K$ and we know that $E^*(m) \to (K, 0)$ as $m \to m_+$.

It is a standard result of graphical predator–prey theory that the equilibrium E^* is locally asymptotically stable whenever $\nu'(x) < 0$ is fulfilled, i.e. whenever the prey nullcline has negative slope (Rosenzweig and MacArthur 1963). If on the other hand E^* is unstable, the Poincaré–Bendixson theorem implies that there is at least

one cycle surrounding E^*. To rule out the existence of cycles in the case when E^* is locally asymptotically stable we additionally need the following assumption:

(C) $(x - x^*)(\psi(x) - \psi(x^*)) > 0$ for $0 < x < K, x \neq x^*$,

where $\psi(x) = -v''(x)\rho(x)^2/\rho'(x)$. This additional assumption allows the application of Dulac's classical theorem for the nonexistence of closed orbits to system (2)–(3). Liu (2005) has used this approach to show that the Gause-type model (2)–(3) has no cycles if and only if the unique equilibrium E^* is located on a downslope of the prey nullcline $v(x)$. As a corollary this extends the local asymptotic stability of E^* to global stability.

Corollary 1 *Under assumptions (A)–(C), the equilibrium E^* is globally stable if and only if $v'(x^*) \leq 0$.*

While assumption (C) has no straightforward biological interpretation, we note that it is fulfilled for many of the usual choices for the prey growth term g and predation rate ρ found in the literature. Corollary 1 immediately implies as a necessary condition for the occurrence of a hydra effect that the coexistence equilibrium E^* has to be unstable.

Proposition 3 *If $v'(x) \leq 0$ for all $0 < x < K$, then under assumptions (A)–(C) a hydra effect of the predator population does not occur.*

As a first very simple application we consider the following well-known example.

Example 1 A hydra effect does not occur in the Lotka–Volterra predator–prey model with logistic prey growth (Volterra 1931) and linear functional response

$$g(x) = g_1(x) = r\left(1 - \frac{x}{K}\right),$$
$$\rho(x) = \rho_1(x) = ax.$$

The prey nullcline

$$v(x) = \frac{r}{a}\left(1 - \frac{x}{K}\right)$$

is linear with negative slope $-r/(aK)$ and the unique equilibrium is always globally stable. Thus, $\phi_y(m) = v(m)$ decreases linearly for increasing mortality rate m.

Therefore, in terms of predator mean density, the interesting parts of the prey nullcline are the intervals for which it has a positive slope and the corresponding equilibrium is unstable. As mentioned, in this case the equilibrium is surrounded by at least one cycle which lies in the strip $0 < x < K$ and $0 < y < \infty$.

The following proposition relates the predator mean density to the prey nullcline $v(x)$. It will allow us to give an upper bound for ϕ_y, which can subsequently be used to derive a sufficient condition for the occurrence of a hydra effect in the predator population.

Lemma 1 *For any solution $Y(t, \xi)$ of (2)–(3) starting at strictly positive initial conditions the mean predator density is given by*

$$\phi_y(\xi) = \frac{1}{T} \int_0^T \nu(x) \, d\tau,$$

where either x is the prey component of a stationary solution or it is cyclic with period T. This implies

$$\min\{\nu(x(t)) | t \in [0, T]\} \leq \phi_y(\xi, m) \leq \max\{\nu(x(t)) | t \in [0, T]\},$$

with equalities if and only if x is stationary.

Proof First observe that using Eq. (2), we can write the predator component of any solution as

$$y = x \frac{g(x)}{\rho(x)} - \frac{\dot{x}}{\rho(x)} = \nu(x) - \frac{\dot{x}}{\rho(x)}.$$

The Poincaré–Bendixson theorem tells us that the solution $Y(t, \xi)$ will either approach the unique equilibrium $E^* = (x^*, y^*)$ or a cycle C surrounding E^*. This implies $\xi \in A(E^*)$ or $\xi \in A(C)$ and by Proposition 1 it suffices to consider the mean value of the equilibrium E^* or the cycle C, respectively. If it approaches E^* the result is immediate, since by Proposition 2(i) the mean value is $\phi_y(\xi) = y^* = \nu(x^*)$. Now assume that Y approaches a cycle $C = (x, y)$ with period T. Applying Proposition 2(ii) for the mean value of cycles yields

$$\phi_y(\xi) = \frac{1}{T} \int_0^T y \, d\tau = \frac{1}{T} \int_0^T \nu(x) \, d\tau - \frac{1}{T} \int_0^T \frac{\dot{x}}{\rho(x)} \, d\tau$$

and using integration by substitution for the rightmost integral we obtain

$$\phi_y(\xi) = \frac{1}{T} \int_0^T \nu(x) \, d\tau - \int_{x(0)}^{x(T)} \frac{1}{\rho(s)} \, ds.$$

Now, since C is a cycle with $x(0) = x(T)$ the last integral vanishes, giving the result. The lower and upper bounds follow immediately. ∎

The simple result that the mean predator density can be expressed in terms of the prey nullcline immediately implies our main result, which states that the necessary condition $\nu'(x) > 0$ is in fact sufficient for the occurrence of a hydra effect in the general model (2)–(3).

Theorem 1 *Under assumptions (A)–(C), a hydra effect of the predator y occurs if and only if there exists a $0 < x < K$ so that $v'(x) > 0$.*

Proof First note that assumption (A) implies $v'(K) < 0$, that is, the prey nullcline crosses the prey axis from above at $x = K$. Now let $v'(x) > 0$ for some $0 < x < K$. Thus $v(x)$ has at least one local maximum at some point $x_0 < K$ with $x_0 = x^*(m_0)$. Then, due to Corollary 1 we have $\phi_y(\xi, m_0) = v(x_0)$ for all $\xi \in \mathbf{R}_{>0}$. Now assume that this is the only extremum of the prey nullcline v. Then the result follows from Lemma 1, since $\phi_y(\xi, m) < v(x_0) = \phi_y(m_0)$ for all $\xi \in \mathbf{R}_{>0}$ and all $m < m_0$. If on the other hand there is more than one local extremum of the prey nullcline, without loss of generality we can assume that there is a minimum at x_1 and a maximum at $x_2 > x_1$, so that $v'(x) > 0$ for $x_1 < x < x_2$. With $x_1 = x^*(m_1)$ and $x_2 = x^*(m_2)$ this implies $\phi_y(m_1) = v(x_1) < v(x_2) = \phi_y(m_2)$.

Thus, although the equilibrium is never actually attained in the case $v'(x) > 0$ our result implies that an increase in predator equilibrium density is nevertheless a necessary and sufficient condition for the occurrence of a hydra effect in the predator population. Accordingly, the remark by Abrams (2009, p. 436) concerning a special case of system (2)–(3) that "the average predator population size need not change in the same direction as the equilibrium" should not be taken to imply that the mean predator abundance does not follow an increase in its equilibrium abundance at all, since it has to do so at least for a certain range of mortality rates.

Note that Theorem 1 is essentially an indirect result in the sense that it is not necessary to know how exactly solutions are affected by changes in the mortality rate, i.e. how the amplitude of a cycle changes when the mortality rate is increased.

4.2 Examples and the quantification of the magnitude of a hydra effect

Probably the simplest models which fulfill the requirement of Theorem 1 and which thus allow for a hydra effect to occur are those where the prey nullcline is given by a quadratic polynomial. A very important representative of this type of model is the focus of the next example.

Example 2 Consider a model with logistic prey growth $g(x) = g_1(x)$ and hyperbolic or Holling type II predation term

$$\rho(x) = \rho_2(x) = \frac{ax}{h+x}.$$

This well-known Rosenzweig–MacArthur model (1963) has been a cornerstone of predator–prey ecology over the last decades. The prey nullcline of this model is given by the quadratic polynomial

$$v(x) = \frac{r}{a}\left(1 - \frac{x}{K}\right)(h + x).$$

This nullcline has a unique maximum at prey density $x_0 = \frac{1}{2}(K - h)$, that is $v'(x_0) = 0$, and the equilibrium E^* is globally stable for $x^*(m) \geq x_0$. A supercritical Hopf bifurcation occurs at $x^*(m_0) = x_0$ (Kuznetsov 1995, p. 93) and for $x^*(m) < x_0$ the

equilibrium is unstable, surrounded by a unique stable limit cycle which attracts all solutions except for E^* (Liou and Cheng 1988). Theorem 1 tells us that a hydra effect occurs in the Rosenzweig–MacArthur model, and we can in fact quantify the magnitude of the hydra effect for this example. If the predator mortality rate is increased from 0 to the Hopf-bifurcation value m_0, the corresponding increase in mean predator density is at least

$$v(x_0) - v(0) = \frac{r}{a}\left(h + \frac{(K-h)^2}{4K}\right) - \frac{rh}{a} = \frac{r(K-h)^2}{4Ka}.$$

This is the difference between the maximum value of the prey nullcline and the value at its intersection with the predator axis at $x = 0$. To see this, let $m < m_0$ and T be the period of the unique asymptotically stable cycle Y. Using Lemma 1, we can bound the mean predator density of this limit cycle from above in terms of the mean prey density by

$$\phi_y(m) = \frac{1}{T}\int_0^T v(x)\,d\tau = -\frac{r}{aK}\frac{1}{T}\int_0^T x^2\,d\tau + \frac{r}{a}\left[\left(1-\frac{h}{K}\right)\phi_x(m) + h\right]$$

$$< \frac{r}{a}\left[\left(1-\frac{h}{K}\right)\phi_x(m) + h\right].$$

Note that a similar estimate can in fact be made for every model with a quadratic prey nullcline. Since $v(0) = \frac{rh}{a}$, it remains to show that $\phi_x(m) \to 0$ for $m \to 0$. Therefore observe that the mean intrinsic growth of the predator along the periodic orbit vanishes

$$\frac{1}{T}\int_0^T [\varepsilon\rho(x) - m]\,d\tau = \frac{1}{T}\int_0^T \frac{\dot{y}}{y}\,d\tau = \frac{1}{T}[\log(y(T)) - \log(y(0))] = 0$$

and we obtain

$$\frac{1}{T}\int_0^T \rho(x)\,d\tau = \frac{m}{\varepsilon}.$$

This simply reflects that the average numerical response of the predator along the periodic orbit exactly outweighs its losses due to mortality during one cycle. Thus

$$\frac{1}{T}\int_0^T \rho(x)\,d\tau \to 0 \quad \text{for } m \to 0,$$

where T in general depends on m. Clearly, any cycle will attain a maximum prey value $x_+ > x^*$ during one cycle. The claim follows immediately if $x_+ \to 0$ for $m \to 0$,

since $\phi_x(m) < x_+$ always holds. Now assume that x_+ does not tend to zero for vanishing predator mortality m. Consider $\ell(x) = cx$ with $c = \rho(x_+)/x_+ > 0$. Then $\ell(x_+) = \rho(x_+)$ and $\ell(x) \leq \rho(x)$ on $0 \leq x \leq x_+$, since ρ is concave downwards. Therefore

$$\frac{1}{T} \int_0^T \rho(x)\, d\tau \geq \frac{1}{T} \int_0^T \ell(x)\, d\tau = c\phi_x(m),$$

and by comparison $\phi_x(m) \to 0$ for $m \to 0$. This result shows that low predator mortality rates are in any case not beneficial for the prey species.

In conclusion, we have seen that for a vanishing predator mortality rate the mean predator density tends to some value smaller than $\nu(0)$. Thus, if m is increased from 0 to the bifurcation value m_0 for which x^* intersects the prey nullcline at its maximum, the mean predator density has to increase at least from $\nu(0)$ to $\nu(x_0)$. A numerical simulation is shown in Fig. 1a. For m very small the mean predator density ϕ_y is very close to $\nu(0)$ and it increases over the whole range of mortality rates for which the unique equilibrium is unstable. Once the unique equilibrium becomes stable at m_0 via the Hopf bifurcation, the predator mean density coincides with $\nu(x^*)$ and it decreases until the predator goes extinct.

Remark 1 In the special case of slow predator and fast prey dynamics, the mean predator abundance in the cyclic regime has been derived to be $\phi_y(m) = \nu(0) = rh/a$ by Dercole et al. (2006). This value is independent of the predator mortality rate and it only holds for the singular limit cycle obtained from slow–fast dynamics. Thus, in the slow–fast special case we have $\phi_y(m) = rh/a$ for $m < m_0$ and $\phi_y(m) = \nu(m)$ for $m \geq m_0$. This implies a discontinuous or "sharp increase" (Dercole et al. 2006, Appendix A4) in mean predator abundance when the system moves from the cyclic to the stationary regime via an increase in predator mortality rate. This corresponds to a non-smooth hydra effect in our terminology and the increase at the Hopf bifurcation point is exactly the value derived in the previous example, namely the difference $\nu(m_0) - \nu(0)$.

Remark 2 The previous example also has interesting implications for the theory of harvesting. Consider that the predator population in the previous example has a natural mortality rate $\bar{m}$ and is harvested with constant effort q. Then the combined mortality rate of the predator is $m = \bar{m} + q$ and the long-term mean yield is $H = q\phi_y(m)$. Now, first, the existence of a hydra effect implies that the mean yield H depends nonlinearly on the harvesting effort q, since ϕ_y increases with q. Second, it implies that if the harvested predator population is in the cyclic regime, e.g. $m < m_0$, the harvesting effort should always be increased in order to increase the mean yield since the mean predator density ϕ_y is maximized at $m = m_0$. It also complements previous work on harvesting in the Rosenzweig–MacArthur model and in tritrophic food chains (de Feo and Rinaldi 1997; Gragnani et al. 1998). In particular, Gragnani et al. (1998) state simple operating rules for the nutrient supply of a harvested population in order to maximize the mean yield, which can be reformulated in the context of the hydra
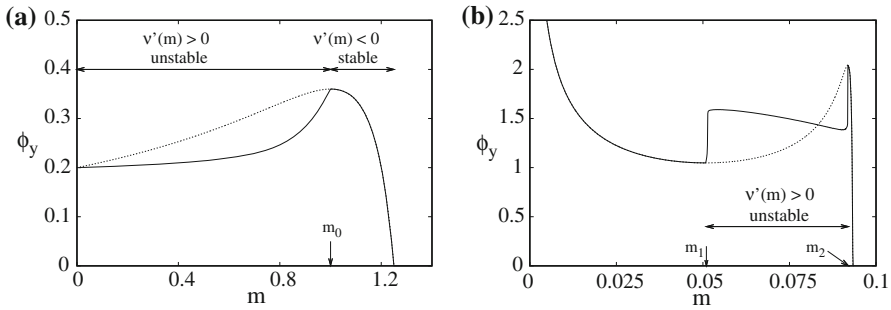
(a)

(b)

Fig. 1 Mean predator population density (*solid line*) versus predator mortality for **a** the model with a type II functional response (Example 2) and **b** the model with a type III functional response (Example 3). Predator density at the unique equilibrium (*dashed line*) coincides with the mean value when the equilibrium is stable and differs from the mean value when it is unstable. The *arrows* indicate the location of Hopf bifurcation points

effect in the following way: if a harvested predator experiences a hydra effect and the underlying predator–prey system is cyclic, then increase the harvesting effort.

In Example 2 numerical simulations indicate that the mean predator density $\phi_y(m)$ is strictly increasing on the whole interval of mortality rates for which $v'(m) > 0$ is fulfilled. However, as has already been observed in numerical simulations by Abrams (2009), in some cases the overall trend of increasing mean predator density may be reversed by significant intermediate intervals of decreasing predator mean densities. At this point it is important to note that Theorem 1 essentially only states that $\phi_y(m)$ has to increase *somewhere* on the interval of mortality rates for which $v'(m) > 0$ is fulfilled and that it has to do so at least in the vicinity of a maximum of the prey nullcline. The next example illustrates the case of alternating intervals of increasing and decreasing predator mean densities.

Example 3 Let $g(x) = g_1(x)$ be of the logistic type again and let the predation term be of Holling type III

$$\rho(x) = \rho_3(x) = \frac{ax^2}{h + x^2}.$$

This model has been analyzed by Yodzis (1989). The prey nullcline $v(m)$ has two extremal points, a minimum at some mortality rate m_1 and a maximum at some $m_2 > m_1$. A numerical example for this model is shown in Fig. 1b. As expected, intervals of increasing predator mean density occur, when the unique equilibrium is unstable and surrounded by a limit cycle. There are two distinct jumps in mean population density close to the two Hopf bifurcations occurring at the two mortality rates $m_1 < m_2$. Shortly after the second Hopf bifurcation at m_2, a sudden collapse of the predator population occurs for a relatively small further increase of the mortality rate.

4.3 Allee effects and non-smooth hydra effects

Species with a strong Allee effect are especially prone to cause a hydra effect in purely prey-dependent predator populations. The presence of a strong Allee effect means that small populations below a critical minimal viable population size (Allee threshold) go extinct. This can be caused, e.g., by a shortage in mating partners and fertilization opportunities at low densities, inbreeding or reductions in the effectiveness of group activities such as anti-predator defense or social care (Allee 1931; Courchamp et al. 2008). Here, a predator with a low mortality rate may suppress the prey population below its Allee threshold, thereby causing the extinction of both species. Translating this scenario into a system of differential equations, this implies that at sufficiently low predator mortality rates attracting strictly positive solutions do not exist but may emerge only at higher mortality rates, thereby giving rise to a non-smooth hydra effect.

For a simple general setting with an Allee effect, consider the basic framework given by system (2)–(3). We drop assumption (C) and extend assumption (A) slightly by assuming that there is an Allee threshold $0 < K_- < K$, such that $g(x) < 0$ for $0 < x < K_-$ and $g(x) > 0$ for $K_- < x < K$. This assumption corresponds to a strong Allee effect of the prey population, with negative growth rates at low prey densities. This implies $\nu(m) < 0$ for $0 < m < m_-$ and $\nu(m) > 0$ for $m_- < m < m_+$. Thus, for the mean predator density we have $\phi_y(m) = 0$ for all $0 < m \leq m_-$, since no strictly positive solutions exist at all. On the other hand, strictly positive attractive solutions may exist for $m_- < m < m_+$ and indeed they surely exist whenever $\nu'(m) < 0$ is fulfilled, since in this case the unique equilibrium E^* is locally stable. And since the prey nullcline crosses the prey axis from above at $x = K$, it has negative slope at least in a neighborhood of K, which implies $\phi_y(m) > 0 = \phi_y(m_-)$ for some $m_- < m < m_+$.

Example 4 Consider a model with the following growth and predation terms (Conway and Smoller 1986; Bazykin 1998; Wang et al. 2011)

$$g(x) = g_4(x) = r(1 - x)(x - K_-),$$
$$\rho(x) = \rho_4(x) = ax.$$

The predation term is of simple Lotka–Volterra form, while the growth term implies an Allee effect with carrying capacity $K = 1$ and Allee threshold $0 < K_- < 1$. The system possesses a unique positive equilibrium E^* which exists for $m_- = \varepsilon a K_- < m < \varepsilon a = m_+$. A numerical simulation of the change of the predator mean density in response to its mortality rate is presented in Fig. 2. The behavior of the mean value ϕ_y reflects that below some bifurcation value $m_c > m_-$ no strictly positive solutions exist, this is the extinction region in Fig. 2. There is a sudden increase in predator mean density at m_c, where a strictly positive limit cycle arises via a global bifurcation (van Voorn et al. 2007). At the Hopf bifurcation value m_0 the mean value coincides with the equilibrium E^* which is stable for all $m > m_0$. For a further increasing predator mortality the mean density follows the downslope of the prey nullcline until the predator goes extinct again.
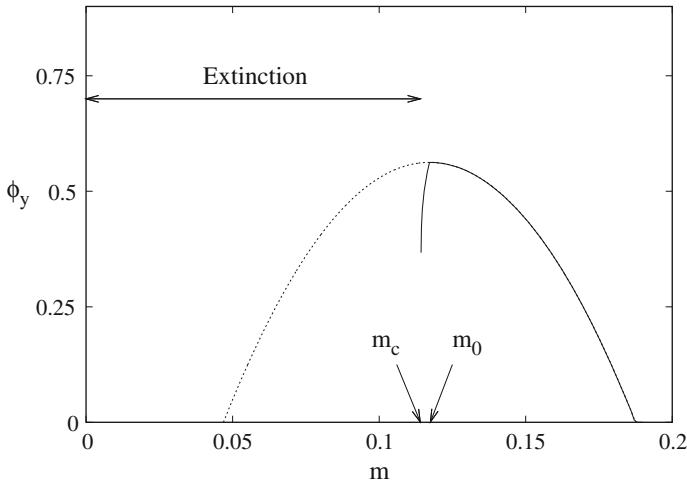
Fig. 2 Mean predator population density (*solid line*) versus predator mortality for the model in Example 4 with an Allee effect in the prey population. Predator density at the unique equilibrium (*dashed line*) coincides with the mean value when the equilibrium is stable and differs from the mean value when it is unstable. The *arrow* labeled with extinction indicates the regime, where no attracting strictly positive solutions exist. m_c refers to the global bifurcation in which a limit cycle appears. m_0 denotes the parameter value where the limit cycle disappears in a Hopf bifurcation

5 Hydra effect in a three-dimensional model

The general two-species model (2)–(3) gives rise to a unique equilibrium, whose stability is easily determined. This was exploited to derive elementary conditions for the occurrence of a hydra effect of the predator population. In contrast to this, the situation becomes considerably more complicated if there is more than one pure consumer of the prey x. The problems arise mainly due to the fact that in contrast to the two-dimensional case (2)–(3), such systems do not allow for stable coexistence at a unique equilibrium of all species. Nevertheless, coexistence of all species is possible in the form of strictly positive nonstationary solutions. The existence of such solutions for certain systems of two pure predators and one prey has been proved by McGehee and Armstrong (1977), which has been extended by Zicarelli (1975) to the case of an arbitrary number of predators coexisting on one prey species. For an illustrative example, we will focus on one particular system, which has been proposed by Armstrong and McGehee (1980).

Example 5 The pure coupled resource–consumer equations for a Lotka–Volterra-type predator y, a Holling-type II predator z and the shared logistically growing prey x read

$$\dot{x} = \left[r \left(1 - \frac{x}{K} \right) - a_1 y - \frac{a_2 z}{h + x} \right] x, \tag{4}$$

$$\dot{y} = [\varepsilon_1 a_1 x - m_y] y, \tag{5}$$

$$\dot{z} = \left[\varepsilon_2 \frac{a_2 x}{h + x} - m_z \right] z. \tag{6}$$

Note that the predator–prey subsystems on the invariant planes $(x, y, 0)$ and $(x, 0, z)$ are of Gause-type. A hydra effect never occurs in the Lotka–Volterra subsystem (x, y), but a hydra effect always occurs in the (x, z) Rosenzweig–MacArthur subsystem, cf. Examples 1 and 2, respectively. Due to the lack of strictly positive stationary solutions however, these results cannot be easily extended to the full two-predator and one-prey system. In the full three-dimensional system, complicated periodic and chaotic solutions may be observed, as well as coexisting alternative attractors (Abrams et al. 2003; Sieber and Hilker 2011).

Let $E_y^* = (x_y^*, y^*, 0)$ and $E_z^* = (x_z^*, 0, z^*)$ denote the semi-trivial equilibria in the $(x, y, 0)$ and $(x, 0, z)$ predator–prey subsystems, respectively. A necessary condition for the existence of strictly positive solutions is $x_z^* < x_y^*$, since otherwise the semi-trivial equilibrium E_y^* becomes globally stable. Assume now that a strictly positive solution exists and that it is periodic with period T. In this case, by integrating Eq. (5) from 0 to T we immediately obtain the mean prey density along this periodic orbit as

$$\phi_x(m_y) = \frac{m_y}{\varepsilon_1 a_1} = x_y^*.$$

The Lotka–Volterra predator y completely determines the mean prey density in the full three-dimensional predator–prey system, regardless of the biological and ecological parameters of the Holling predator z. In fact, this is of course the case with any Lotka–Volterra predator in any purely prey-dependent predator–prey system with arbitrary many predators. The presence of a single Lotka–Volterra predator in an ecological model community determines the mean amount of prey at any time and it also implies the well-known result that two or more linear predators cannot coexist on a single shared prey (McGehee and Armstrong 1977).

So while we cannot expect to derive an analytical expression for the mean predator densities of system (4)–(6), we exactly know how much prey there is on average. This can be used to derive upper bounds for both predator mean densities. In a similar fashion as in the two-dimensional Gause-type model, we obtain from Eq. (4)

$$\phi_y < r - \frac{\phi_x(m_y)}{K} = r - \frac{m_y}{\varepsilon_1 a_1 K},$$
$$\phi_z < \frac{r}{a_2}\left[\left(1 - \frac{h}{K}\right)\phi_x(m_y) + h\right] = \frac{r}{a_2}\left[\left(1 - \frac{h}{K}\right)\frac{m_y}{\varepsilon_1 a_1} + h\right].$$

Apparently, an increase in the prey carrying capacity K seems beneficial for the whole ecological community, since it increases the upper bounds for both predator mean densities. However, in the case of unlimited carrying capacity $K \to \infty$, the upper bounds for both predators approach finite values. As one would expect, the mortality rate m_y adversely affects the upper bound for the mean value of predator y on the one hand and increases the upper bound for ϕ_z on the other hand. The mortality rate m_z however does not change the upper bounds at all, again reflecting the dominance of the linear predator. Also, the first inequality gives another necessary condition for the existence of strictly positive solutions. The mean value of predator y can only be positive, if $x^* < rK$, giving the complete necessary condition $x_z^* < x_y^* < rK$ for
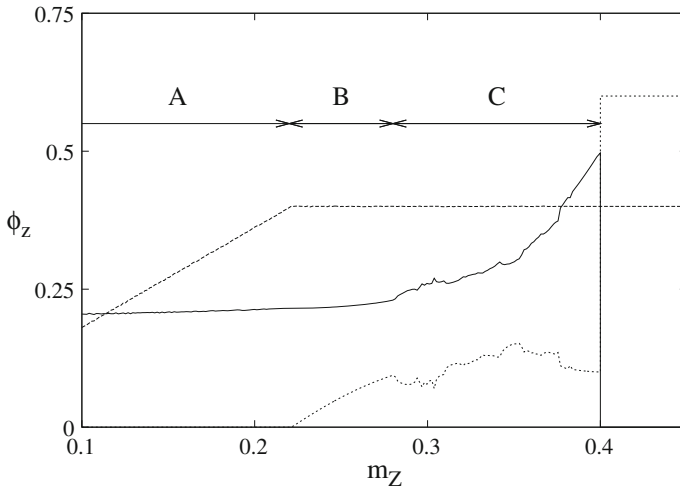
Fig. 3 Mean population densities (prey x: *dashed*; linear predator y: *dotted*; nonlinear predator z: *solid*) versus predator z mortality m_z for the three-species exploitative competition model (4)–(6). Regimes of qualitatively different system dynamics are indicated by *arrows*. *A* Cyclic coexistence of prey x and nonlinear predator z (Rosenzweig–MacArthur subsystem). *B* Cyclic coexistence of all three species. *C* Alternative cyclic and chaotic attractive solutions. Sudden extinction of the nonlinear predator z at $m = 0.4$. For mortality rates larger than 0.4 stationary coexistence of prey x and linear predator y. Parameters are $r = 1, K = 1, a_1 = 1, a_2 = 0.5, h = 0.1, m_y = 0.4, \varepsilon_1 = \varepsilon_2 = 1$

strictly positive solutions. For a further analysis of the predator mean densities, we now turn to numerical simulations.

In Fig. 3 a numerical approximation of the population mean densities for varying predator z mortality m_z is shown for model (4)–(6). Note that varying m_z only affects the stationary point x_z^* in the (x, z) subsystem, while x_y^* remains constant. If a small amount of predator y is introduced into the system, it is clearly not able to establish unless a critical mortality rate m_- is exceeded. This is region A in Fig. 3. After establishment of predator y, in region B we observe cyclic coexistence of all three species and the corresponding mean prey density remains fixed at $\phi_x(m_z) = x_y^*$ as expected. Clearly, in this region an increasing predator z mortality m_z is beneficial for the first predator y, reflected by an increasing predator mean value $\phi_y(m_z)$.

In region C, at least two alternative attractors may coexist, both of which may be periodic or chaotic (Sieber and Hilker 2011). Both predator mean densities show a more irregular behavior in this region with several small magnitude non-smooth hydra effects occurring when the fixed initial condition switches from one basin of attraction to another or when one of the attractors vanishes in a boundary crisis.

Over the whole range of mortality rates, however, the predator z mean density $\phi_z(m_z)$ clearly shows a hydra effect, which is even more pronounced after predator y has established in the system, leading to a doubling in its initial value until the mortality rate m_z reaches a critical value. This critical value of m_z is given by

$$m_z = \frac{\varepsilon_2 a_2 m_y}{\varepsilon_1 a_1 h + m_y} \Leftrightarrow x_y^* = x_z^*. \tag{7}$$

Table 1 Hydra effects occur in various nonlinear standard predator–prey models

Model	Reference	Biological mechanism	Hydra effect
Example 1	Volterra (1931)	Linear functional response	No
Example 2	Rosenzweig and MacArthur (1963)	Type II functional response	Yes
Example 3	Yodzis (1989)	Type III functional response	Yes
Example 4	Bazykin (1998)	Prey with strong Allee effect	Yes, non-smooth
Example 5	Armstrong and McGehee (1980)	Two predators (linear/nonlinear)	Yes, smooth and non-smooth

If m_z is increased over this critical value, a sudden extinction of the predator z population can be observed. This extinction can easily be understood in terms of stability of the boundary equilibria, since the stationary solution E_y^* in the (x, y) subsystem becomes globally stable for $x_y^* < x_z^*$. However, from a biological viewpoint, this sharp threshold phenomenon is an interesting effect and even more so, since the increasing predator mean density right before the catastrophic crash gives the impression of a healthy population.

6 Discussion

The analytical and numerical results above show that hydra effects are a typical feature of Gause-type predator–prey systems, whenever the model allows for an unstable non-trivial equilibrium. Table 1 summarizes the results from the examples that have been discussed in the text.

The examples have also shown that one can distinguish between two qualitatively different types of hydra effects. A smooth hydra effect is due to a smooth change in the shape of an attractor, like changes in the amplitude of a limit cycle as in Examples 2 and 3. A non-smooth hydra effect, by contrast, is associated with an abrupt change in the long-term behavior of a solution starting at a particular initial condition. This change can either be due to a global bifurcation as in Example 4, where a strictly positive attractive solution arises suddenly at a certain mortality rate. Alternatively, the long-term behavior of a solution might change abruptly because changing the mortality rate alters the shape of the basins of attraction of coexisting attractors and the initial condition switches from one basin of attraction to another one as in Example 5.

The hydra effect is closely associated with the imminent collapse of the respective species for which the hydra effect is observed. This is due to the fact that an increase in predator mean density has to occur right before maximal predator population sizes are reached, after which a further increase of the mortality rate necessarily leads to a decline in population size. The population collapse is most pronounced and unexpected in the case of two predators coexisting on one shared prey species (Example 5), where there is a distinct critical mortality rate at which the sudden collapse of the seemingly healthy predator population occurs. In the case of just one predator, the imminent extinction of the predator is indicated by a continuous but nevertheless very rapid decline in mean population density in response to further increasing mortality rate (cf. Fig. 1). This has the implication that the observation of mean population densities

alone may lead to false assumptions regarding the persistence of a population. In fact, catastrophic crashes are inherently present in models with purely prey-dependent predators. This is especially of concern when the predator population is harvested, see Remark 2.

The general Gause-type model (2)–(3) is a cornerstone of predator–prey ecology. It has been used in various specific forms and the results presented here show that hydra effects are typically present in all of these variants, except for the simplest Lotka–Volterra models. It is therefore striking that direct evidence for the existence of hydra effects in natural populations is rare. This lack of empirical evidence has partly been attributed to the lack of appropriate observations (Abrams 2009). Another cause for the apparent discrepancy at least between the predator–prey models investigated here and empirical data, however, might be attributed to shortcomings of the general model (2)–(3).

A prominent peculiarity of the model is that the intrinsic growth rate of the predator does not depend on its own density. This feature greatly simplifies the analysis of the model, but given that "[i]n real life, we never expect to encounter *pure* resource–consumer systems" (Turchin 2003, p. 36) it is certainly worthwhile to address the problem of hydra effects in non-pure resource–consumer systems. An obvious way to make the predator growth rate dependent on its own density is to add a quadratic closure term reflecting intraspecific competition to the predator equation (3), thereby implicitly introducing an upper density bound for the predator population. A corresponding variant (Bazykin 1998, p. 67) of the Rosenzweig–MacArthur model (cf. Example 2) is inherently more stable (Turchin 2003, p. 98) and thus the parameter range for which a hydra effect might occur is greatly reduced. In addition to quadratic closure, there are other biologically meaningful mechanisms which make the predator growth rate dependent on its own density, such as ratio-dependent predation (Abrams and Ginzburg 2000) and predator interference (Beddington 1975; DeAngelis et al. 1975). While the relative importance of these factors is usually difficult to measure in real populations, it is an interesting question for future research whether they may resolve at least in part the apparently paradoxical phenomenon of hydra effects in predator–prey models.

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