A Predator–Prey Model with Optimal Suppression of Reproduction in the Prey

MATS GYLLENBERG
Department of Mathematics, University of Turku, FIN-20500 Turku, Finland

ILKKA HANSKI
Department of Zoology, University of Helsinki, FIN-00100 Helsinki, Finland

AND

TORSTEN LINDSTRÖM
Department of Mathematics, University of Örebro, S-70130 Örebro, Sweden

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ABSTRACT

Several time-discrete ecological models are formulated and analyzed. Common to these models is that a trade-off between reproductive effort and competitive ability is assumed. We investigate how behavioral adjustment (suppression of reproduction) affects the population dynamics.

1. INTRODUCTION

Numerous theoretical and empirical studies have elucidated the consequences of predation risk on the foraging behavior of animals (e.g., [1, 2]). A much less studied but equally interesting question is to what extent predation risk affects the breeding behavior of prey individuals. This is an intriguing question because it directly links behavior and population dynamics. An expanding body of empirical literature demonstrates that high risk of predation may lead to suppressed reproduction in the prey [3–7], but to our knowledge there are no theoretical analyses of the population dynamic consequences of optimal breeding behavior of prey in the presence of high risk of predation. The empirical system that has motivated our study is the interaction between microtine rodents and their mustelid predators in northern Europe [8]. Recent studies have demonstrated that both maturation of young voles and the early development of the offspring of older voles are affected by risk of predation [3].
The main objective of this paper is to formulate and analyze a predator–prey model with the possibility of suppressed reproduction in the prey. We commence with a single-species model in which we assume a trade-off between the reproductive effort and competitive ability. If no behavioral adjustment of the rate of reproduction is allowed for, the type with the reproductive rate maximizing the equilibrium population size prevails, regardless of whether the equilibrium point is stable or not. However, when behavioral adjustments are allowed for, the winning type suppresses reproduction, to some extent, whenever the equilibrium is unstable, and this behavior decreases the mean amplitude of population oscillations. We then extend this model to include predation, assuming a trade-off between the reproductive effort and an individual's ability to avoid predation. Optimal adjustment of reproduction by the prey adds to population stability, as measured by the mean amplitude of oscillations. This result supports the main conclusions in [9, 10], where population dynamical consequences of optimal behavior were analyzed using different approaches.

Our paper is organized as follows. In Section 2 we introduce the notions of fixed and adjustable strategy in the single-species case. We find the best fixed strategy and investigate the asymptotic behavior of solutions to a model describing competition between fixed and adjustable strategies. In Section 3 we introduce a new discrete predator–prey model, which can be regarded as a combination of the Ricker model [11], the Nicholson–Bailey model [12], and the continuous Lotka–Volterra model [13, 14]. A mechanistic explanation of the model is included in Section 3. In Section 4 we investigate the dynamics of this discrete predator–prey model, and this study culminates in an important stability theorem. In Section 5 we investigate the dynamical consequences of the optimal suppression of reproduction in the prey. The analytical study of the predator–prey model is supplemented with a numerical study in Section 6. In Section 7 we relate our results to those of other authors and discuss their biological implications. The proofs of the theorems and propositions can be found in Section 8.

2. FIXED AND ADJUSTABLE STRATEGIES IN THE SINGLE-SPECIES CASE

The growth of a semelparous population reproducing at discrete instances can in general be described by the difference equation

$$x' = xR(E),$$

(2.1)

where \(x\) is the population density, \(E\) is the state of the environment at the beginning of a season (immediately after reproduction), and \(x'\) is
the population density at the beginning of the next season. \( R(E) \) is the net reproduction number when the environmental state is \( E \), that is, the expected number of offspring born to an individual. In this paper we are concerned with the effects of density-dependent competition and predation upon population dynamics, and therefore we choose, in the single-species case, simply the population density as the environmental state. In the predator-prey model considered in Sections 3–5 the environmental state of the prey will be described by the sum of the prey density and the predation pressure. In both cases it is natural to assume that \( R \) is a decreasing function tending to zero as \( E \) tends to infinity. To be specific we choose

\[
R(E) = \beta \exp(-kE).
\]  

(2.2)

Observe that the model (2.1), (2.2) supplemented by \( E = x \) is nothing but the well-known Ricker model, first introduced in [11]. The parameter \( k \) in (2.2) measures the strength of the density dependence or the competitive ability, and \( \beta \) can be interpreted as the average clutch size at low density, when there is no negative effect of density on reproduction. (We use the term \textit{clutch} as shorthand for a "batch of offspring born at the same time," with no intention of restricting the results to species for which "clutch" is generally used in the biological literature.)

Consider now competition between two asexually reproducing types \( x \) and \( y \) of the same species. We assume that the types have different parameters \( \beta \) and \( k \) and that the environment is given by the total population density. The population density dynamics is then described by the model

\[
x' = xR_1(E),
\]

(2.3a)

\[
y' = yR_2(E),
\]

(2.3b)

\[
E = x + y,
\]

(2.3c)

\[
R_i(E) = \beta_i \exp(-k_iE), \quad i = 1, 2.
\]

(2.3d)

We prove below that the type with the net reproduction number that maximizes the equilibrium population size will outcompete all other types. This conclusion is a well-known principle of natural selection going back at least as far as [15]. We prove the result in a general setting that includes the cases where the equilibrium point is unstable and the dynamics are cyclic or chaotic.

\textit{Proposition 2.1}

Let \( \beta_1, \beta_2 > 1 \), and let \( x^* = \log \beta_1 / k_1 \) and \( y^* = \log \beta_2 / k_2 \) be the unique solutions of the equations \( R_1(x^*) = 1 \) and \( R_2(y^*) = 1 \), respectively.
Then \((x^*, 0)\) and \((0, y^*)\) are fixed points of system (2.3). If \(x^* > y^*\), then the \(x\) axis attracts every point not on the \(y\) axis; and if \(x^* < y^*\), then the \(y\) axis attracts every point not on the \(x\) axis.

We now assume a trade-off between reproductive effort and competitive ability by making \(k\) a function of \(\beta\). We assume that offspring are produced in clutches, that larger values of \(\beta\) correspond to larger clutches, and that individuals producing small clutches do better in competition than individuals producing large clutches. This assumption has substantial empirical support for many organisms [16] and requires \(k\) to be an increasing function of \(\beta\). The competition model now takes the form

\[
x' = x\beta_1 \exp\left[-k(\beta_1)E\right], \tag{2.4a}
\]

\[
y' = y\beta_2 \exp\left[-k(\beta_2)E\right], \tag{2.4b}
\]

\[
E = x + y. \tag{2.4c}
\]

Proposition 2.1 implies that the type with the largest equilibrium density in the absence of the other type will outcompete the other. Since this equilibrium is given by

\[
h(\beta) = \frac{\log \beta}{k(\beta)}, \tag{2.5}
\]

we infer that the type with largest \(h(\beta)\) will win in intraspecific competition. For physiological reasons, individuals cannot produce an arbitrarily large number of offspring. We denote the upper bound of the clutch size by \(M\). It seems reasonable to assume the existence of a unique optimal clutch size \(\hat{\beta}\). Mathematically this amounts to requiring that the function \(h\) defined by (2.5) have a unique global maximum \(\hat{\beta} \in (0, M]\).

We make the following assumptions about \(k\).

(B.I) \(k: [0, M] \to \mathbb{R}_+\) is positive and increasing.

(B.II) The function \(\beta \to (\log \beta)/k(\beta)\) has a unique global maximum \(\hat{\beta} \in (0, M]\).

(B.III) \(k \in C^2(0, M)\) and \(\beta k''(\beta) + k'(\beta) > 0\) for all \(\beta \in (0, M] \).

The first two of these assumptions are, as explained above, biologically justified. The significance of the last one will become clear in connection with Propositions 2.2 and 5.1. Notice that the function \(k(\beta) = \beta^p\), \(p > 0\), satisfies (B.I)–(B.III), and this \(k\) will serve as our prototype in the sequel.
The strategy involving $\hat{\beta}$ is best among all fixed strategies, that is, strategies for which individual reproductive behavior does not depend on the current state of the environment. We consider now a strategy in which individuals adjust their clutch size by maximizing their contribution to the next generation, that is, the net reproduction number is given by

$$R_2(E) = \sup_{0 < \beta < M} \beta \exp[-k(\beta)E]. \quad (2.6)$$

Is this strategy better than the fixed one? To answer this question we consider the competition model (2.3) with $R_1$ given by $R_1(E) = \hat{\beta} \exp[-k(\hat{\beta})E]$ and $R_2$ given by (2.6). For ease of reference we repeat the model describing competition between the best fixed strategy and the adjustable strategy:

$$x' = x \hat{\beta} \exp[-k(\hat{\beta})E], \quad (2.7a)$$
$$y' = y \sup_{0 < \beta < M} \beta \exp[-k(\beta)E], \quad (2.7b)$$
$$E = x + y. \quad (2.7c)$$

**PROPOSITION 2.2**

Assume (B.I)-(B.III). Then,

(i) The supremum in (2.6) is a maximum, and for every $E \in \mathbb{R}_+$ it is attained at precisely one $\beta \in (0, M]$. 

(ii) The unique $\beta = \hat{\beta}(E)$ found in (i) defines a continuous function $\hat{\beta}: \mathbb{R}_+ \to (0, M]$ that takes on the value $M$ in $[0, 1/Mk'(M)]$, is strictly decreasing in $[1/Mk'(M), \infty)$ and satisfies

$$\hat{\beta} \left( (\log \hat{\beta})/k(\hat{\beta}) \right) = \hat{\beta}. \quad (2.8)$$

(iii) Put

$$\mathcal{L} = \left\{ (x, y) \in \mathbb{R}_+^2 : x + y = \frac{1}{Mk'(M)} \right\}.$$

The map $(x, y) \mapsto (x', y')$ defined by (2.7) is continuously differentiable on $\mathbb{R}_+^2 \setminus \mathcal{L}$.

Conclusion (ii) says that the type $y$ using the adjustable strategy produces the largest physiologically possible clutches at low population densities $E$. As the population density grows beyond a threshold value
1/\[Mk'(M)], this type starts to suppress reproduction. If the population density is larger than the equilibrium population density \((\log \hat{\beta})/k(\hat{\beta})\), then the type using the adjustable strategy will actually produce smaller clutches than the type \(x\) using the best fixed strategy.

The following theorem is of considerable importance.

**THEOREM 2.3**

Let the assumptions \((B.I)-(B.III)\) hold, and assume that \(P = (x_0, y_0) \in \text{Int} \mathbb{R}^2\). Every point on the segment

\[
x + y = \frac{\log \hat{\beta}}{k(\hat{\beta})}, \quad x \geq 0; \ y \geq 0,
\]

is a fixed point of \((2.7)\). If the \(\omega\)-limit set \(\omega(P)\) of \(P\) is not a subset of the \(y\) axis, then \(\omega(P)\) consists of a single point on the segment \((2.9)\). One has

\[
\frac{y'}{x'} \geq \frac{y}{x},
\]

and the exact location of \(\omega(P)\) depends on the initial state \(P\).

**Remark 2.4.** By the argument used in the proof of Theorem 2.3, it is possible to show that the optimal adjustable strategy amounts to maximization of an individual's share of the offspring in the next generation.

Theorem 2.3 enables us to draw some interesting conclusions. By inequality \((2.10)\), the adjustable strategy always gains ground at the expense of the fixed strategy. Notice that the equilibrium total population density \(x^* + y^* = (\log \hat{\beta})/k(\hat{\beta})\) is the nontrivial fixed point of both the maps

\[
x' = x\hat{\beta} \exp[-k(\hat{\beta})x]
\]

and

\[
y' = y \sup_{0 < \beta < M} \beta \exp[-k(\beta)y]
\]

describing the dynamics of each of the two types in the absence of the other. Theorem 2.3 shows that if the nontrivial fixed point of \((2.11)\) is unstable, then the proportion of individuals using the adjustable strategy increases until a stable fixed point of \((2.7)\) is reached. If all the fixed points of \((2.7)\) are unstable, then the adjustable strategy outcompetes the fixed strategy.
Next we give an example demonstrating that adjustment of reproduction has a stabilizing effect on population dynamics.

**Example 2.5.** Consider the case \( k(\beta) = \beta^p \) and \( M = \hat{\beta} \). We first calculate \( \hat{\beta} \) and get \( \hat{\beta} = \exp(1/p) \). Thus the map (2.11) is given by

\[
x' = x \exp(1/p) \exp(-ex),
\]

and the map (2.12) is given by

\[
y' = \begin{cases} 
   y \exp(1/p) \exp(-ey), & y < 1/pe \\
   y(pey)^{-1/p}, & y > 1/pe.
\end{cases}
\]

If \( 0 < p < 1/2 \), then the map (2.13) has cyclic or chaotic behavior. Observe that the map (2.14) conserves the derivative of the map (2.13) in the fixed point \( 1/pe \), and therefore the linearized stability of the fixed point \( 1/pe \) of the map (2.13) carries over to the map (2.14). It was shown in [17], Proposition 1, pp. 121–122, that if a continuous map \( f \) on a compact interval has no two-periodic points, then every orbit converges to a fixed point of \( f \). The maps (2.13) and (2.14) have bounded orbits and a unique locally stable fixed point for \( p \geq 1/2 \). Moreover, these maps have no two-periodic points, and hence the result mentioned above implies that the locally stable fixed point is in fact (almost) globally stable (it attracts everything except the origin).

Figure 1 demonstrates how adaptive adjustment of reproduction decreases the mean amplitude of oscillations. The amplitude was measured by the standard deviation of log-transformed values after the changes \( \mathcal{X} = ex \) and \( \mathcal{Y} = ey \) in (2.13) and (2.14), respectively. Our example shows that as long as the equilibrium \( 1/pe \) is a global attractor for the map (2.13), this equilibrium is a global attractor for the map (2.14). However, if this equilibrium is unstable, then the mean amplitude of the cyclic or chaotic oscillations in the behaviorally adjustable case (2.14) seems to be smaller than in the case of fixed behavior (2.13). Note that the dominating period (the period corresponding to the maximum of the Fourier spectrum) is 2 during the whole first-period doubling sequence and far beyond it in both cases. The mean amplitude of oscillations and the dominating period are noteworthy variables in this context because they are frequently estimated in empirical studies of rodent population dynamics [8].

### 3. A PREDATOR–PREY MODEL

In this section we derive a discrete predator–prey model that is a variant of the Nicholson–Bailey model with density-dependent prey
dynamics and a long-lived predator. As before, we assume that the prey individuals live for one season only.

As in the preceding sections we use the Ricker model (2.1), (2.2) to describe reproduction and intraspecific competition among the prey. Predation is an extra source of mortality in the prey, and it seems reasonable to incorporate this in the model by adding a term describing "predation pressure" to the definition of the environmental state $E$. We wish to emphasize that the precise way in which predation is taken into account through $E$ is not obvious and that careless discretization of continuous predator–prey models may lead to biologically meaningless models (see Gyllenberg et al. [18]). We therefore derive our predator–prey model by integrating the corresponding continuous Lotka–Volterra model over one season.
During the season, predation takes place continuously according to the linear (type I) functional response $\alpha \gamma x$ and predators die at a constant rate $d$. We make a distinction between the consequences of predator behavior ($\alpha$) and prey behavior ($\gamma$) on predation rate, hence the product of the two parameters (this will become apparent below). The densities $x$ and $z$ of prey and predators, respectively, satisfy the following system of ordinary differential equations:

$$ \dot{x} = -\alpha \gamma x z, \quad \dot{z} = -dz. \quad (3.1) $$

The solution to (3.1) is given by

$$ x(t) = \exp\left[-\frac{\alpha \gamma}{d} z_0 (1 - e^{-dt})\right] x_0, $$

$$ z(t) = \exp\left(-dt\right) z_0, $$

$0 \leq t \leq T$, where $x_0$ and $z_0$ are the initial densities of prey and predators, respectively, and $T$ is the length of the season.

We introduce the new parameters

$$ \mathcal{F} = \exp(-dT), $$

which is the probability that a predator survives the season, and

$$ a = \frac{\alpha}{d} (1 - \mathcal{F}). $$

The number of prey eaten during the season is given by

$$ [1 - \exp(-\gamma az_0)] x_0, $$

and of these

$$ \mathcal{F}[1 - \exp(-\gamma az_0)] x_0 $$

have been digested by predators still alive at the end of the season. We assume that a fraction $m$ of this prey mass is transformed into new predators at the end of the season.

Following the single-species model of Section 2, we assume that there is a relationship between the competitive ability and the reproduc-
tive effort of the prey, and hence we assume that $k$ is an increasing function of $\beta$. We also assume that prey individuals producing large clutches are more vulnerable to predation and hence that the coefficient $\gamma$ in the functional response is an increasing function of $\beta$. To simplify the model we assume that $\gamma = k$.

Assuming that the prey individuals that survived competition and predation produce $\beta$ offspring on average, we arrive at the following discrete model:

$$x' = x\beta \exp[-k(\beta)(x + az)], \quad (3.2)$$

$$z' = m\mathcal{F}[1 - \exp[-k(\beta)az]]x + \mathcal{F}z. \quad (3.3)$$

Observe that Equation (3.2) is of type (2.1), (2.2) with $E = x + az$. The term $az$ can be interpreted as the predation pressure each prey individual is subject to.

We now continue as follows. We analyze the dynamics of the fixed strategy case (3.2), (3.3) for different $\beta < M < \exp(2)$ in Section 4. Here we assume that $\beta = \hat{\beta}$ (see Section 2). The last assumption holds, for instance, if the optimal fixed strategy has outcompeted the other fixed strategies before the predators enter the system. If $k(\beta) = \beta^p$, then the restriction $0 < \hat{\beta} < M < \exp(2)$ implies that $p > 1/2$. In Section 5 we allow the prey to adjust its reproduction as in model (2.12) and compare the dynamics of the adjustable strategy to the dynamics of the fixed strategy in the predator-prey case.

4. DYNAMICS OF THE PREDATOR-PREY MODEL

In this section we give a complete description of the local bifurcations of model (3.2), (3.3) when $\beta$ varies from 0 to $M < \exp(2)$. The restriction on $\beta$ implies that in the Ricker model $x' = x\beta \exp[-k(\beta)x]$ either (if $\beta < 1$) the origin is a globally stable fixed point or (if $1 < \beta < M < \exp(2)$) there is a positive stable fixed point attracting all points except the origin. Hence all oscillations in model (3.2), (3.3), if any occur, are due to the predator-prey interaction, not to oscillations in the Ricker model. We therefore call these oscillations pure predator-prey oscillations.

The case $\beta > \exp(2)$ was studied numerically for the Nicholson-Bailey model with density-dependent host reproduction in [19]. The
conclusion was that if $\beta$ exceeds $\exp(2)$ then an unexpected extinction of the predator can occur, as a result of subcritical flip bifurcation.

**THEOREM 4.1**

Consider system (3.2), (3.3), where the parameters $a$, $m$, $\beta$, $\mathcal{F}$ are positive, $\mathcal{F} < 1$, and $k: (0, M] \rightarrow \mathbb{R}_+$ is increasing.

(i) The origin is a fixed point for all parameter values. It is globally asymptotically stable if $\beta < 1$ and unstable if $\beta > 1$.

(ii) If $\beta > 1$, then $(\log \beta / k(\beta), 0)$ is a fixed point and there are no other fixed points on the boundary of $\mathbb{R}^2_+$ except the origin. $(\log \beta / k(\beta), 0)$ is locally asymptotically stable if $1 < \beta < \exp[(1 - \mathcal{F})/am\mathcal{F}]$ and is unstable if $\exp[(1 - \mathcal{F})/am\mathcal{F}] < \beta$.

(iii) There exists a fixed point $(x^*, z^*) \in \text{Int} \mathbb{R}^2_+$ if and only if $\exp[(1 - \mathcal{F})/am\mathcal{F}] < \beta$ and there are no other fixed points in $\text{Int} \mathbb{R}^2_+$. Assume that $\exp[(1 - \mathcal{F})/am\mathcal{F}] < \beta$, and let $(x^*, z^*)$ be the unique fixed point in $\text{Int} \mathbb{R}^2_+$ provided by (iii).

(iv) If $0 < am < 1$, then $(x^*, z^*)$ is locally asymptotically stable for $\beta < \exp(2)$.

(v) If $am > 1$, then there exists a $\beta^* > \exp[(1 - \mathcal{F})/am\mathcal{F}]$ such that $(x^*, z^*)$ is locally asymptotically stable for $\beta < \beta^*$ and unstable if $\beta > \beta^*$.

(vi) If $\beta^* < \exp(2)$, then the eigenvalues of the Jacobian evaluated at $(x^*, z^*)$ for $\beta = \beta^*$ are complex conjugates located on the unit circle.

Theorem 4.1 calls for some comments. Conclusion (i) states the obvious fact that if the prey's average clutch size $\beta$ is less than 1, then the prey and hence the predator will go extinct. As $\beta$ is increased through 1, a fixed point at $(\log \beta / k(\beta), 0)$ is formed in a saddle-node bifurcation and the prey becomes persistent. A new fixed point in the interior of the state space is formed in a saddle-node bifurcation when $\beta = \exp[(1 - \mathcal{F})/am\mathcal{F}]$ and the predator becomes persistent. We notice that it is the relation between the odds $(1 - \mathcal{F})/\mathcal{F}$ of the predator dying and the number $am \log \beta$ that determines whether the predator is persistent or not.

If the fixed point in the interior of the state space becomes unstable as $\beta$ increases from $\exp[(1 - \mathcal{F})/am\mathcal{F}]$ to $\exp(2)$, then it undergoes at most one bifurcation. By (vi) this bifurcation is a Hopf bifurcation (unless the eigenvalues happen to be some of the first five roots of unity, which is extremely unlikely), and pure bounded predator-prey oscillations occur. A quick observation tells us that $am > 1$ is a necessary condition for pure predator-prey oscillations. The proof of Theorem 4.1 shows that a sufficient condition is that $am\mathcal{F}$ is large enough.

The generic behavior of dynamical systems after a Hopf bifurcation has been studied by several authors; see [20–22] and references therein.
As an especially interesting biological application, we refer to [23]. If we interpret these results for system (3.2), (3.3), we get the following. As $\beta$ is slightly increased above the critical value $\beta^*$, an invariant circle with quasi-periodic behavior appears generically [20]. As $\beta$ is further increased, this quasi-periodic behavior will generically become interspersed with (usually) high-periodic resonances [21, 22].

The likelihood for resonances increases as the parameter $\beta$ is further increased and large intervals with low-periodic behavior can be detected. Simultaneously, the invariant circle formed in the Hopf bifurcation loses its smoothness gradually, and a transition from regular behavior toward chaotic behavior takes place. The fine structure of this transition is extremely complicated and is studied in detail numerically for another system in [24]. Our numerical results, presented in Section 6, agree with the findings of [24].

5. PREDATOR-PREY SYSTEMS AND THE ADJUSTABLE STRATEGY

In this section we take a closer look at the dynamical consequences of the adjustable strategy. We are interested in two questions. Does a type with the ability to adjust its reproduction have an advantage over types that lack this ability? Does the adjustable strategy increase the stability of the dynamics?

To treat the first question we assume that a prey of type $x$ uses the optimal fixed strategy, which, in the absence of predation, was found in Section 2 to set its average clutch size $\beta$ to $\hat{\beta}$, the maximum of $(\log s)/k(s)$. The predator–prey dynamics are thus given by the model

$$
\begin{align*}
x' &= x\hat{\beta}\exp\left[-k(\hat{\beta})(x + az)\right], \\
z' &= m\mathcal{F}\left(1 - \exp\left[-k(\hat{\beta})az\right]\right)x + \mathcal{F}z,
\end{align*}
$$

(5.1)

where, as before, $z$ denotes the predator density.

Consider now another prey type $y$, which can adjust the clutch size $\beta$ according to the present state of the environment. Mathematically we express this by letting $\beta$ be a function $\tilde{\beta}$ of the state $E$ of the environment. We finally combine model (5.1) with (2.7), describing intraspecific competition between two prey types—one ($x$) using a fixed strategy, and the other ($y$) using an adjustable strategy. We obtain

$$
\begin{align*}
x' &= x\tilde{\beta}\exp\left[-k(\tilde{\beta})E\right], \\
y' &= y\tilde{\beta}\exp\left[-k(\tilde{\beta})E\right],
\end{align*}
$$

(5.2a, 5.2b)
\[
z' = mF\left(1 - \exp[-k(\beta)az]\right)x + mF\left(1 - \exp[-k(\beta)az]\right)y + Fz, \tag{5.2c}
\]

\[
E = x + y + az, \tag{5.2d}
\]

where \(\beta = \beta(E)\) is determined by

\[
\tilde{\beta}(E)\exp[-k(\tilde{\beta}(E))E] = \sup_{0 < \beta < M} \beta \exp[-k(\beta)E]. \tag{5.3}
\]

The constant \(M > \beta\) is a physiologically determined upper bound of the clutch size \(\beta\). The idea behind (5.3) is similar to the optimal adjustment (2.6) in the single-species case. The right-hand side of (5.3) is the maximal net reproduction number and the net reproduction number for the type using the adjustable strategy. The assumptions (B.I)–(B.III) guarantee that \(\beta\) is uniquely determined through (5.3), and so the mapping \((x, y, z) \mapsto (x', y', z')\) given by (5.2) is well defined. This is the main content of the following proposition.

**PROPOSITION 5.1**

Let the assumptions (B.I)–(B.III) hold, and put \(E = x + y + az\). Then,

(i) For each \(E \in \mathbb{R}^+\), the relation (5.3) uniquely determines a number \(\tilde{\beta}(E) \in (0, M]\).

(ii) The function \(\tilde{\beta}: \mathbb{R}^+ \to (0, M]\) defined by (5.3) is continuous, constant on \([0, 1/Mk'(M)]\), and strictly decreasing on \((1/Mk'(M), \infty)\). Moreover,

\[
\tilde{\beta}\left(\frac{\log \beta}{k(\beta)}\right) = \beta.
\]

(iii) Put

\[
\mathcal{L} = \left\{(x, y, z) \in \mathbb{R}^3_+: x + y + az = \frac{1}{Mk'(M)}\right\}.
\]

The map \((x, y, z) \mapsto (x', y', z')\) defined by (5.2) is continuously differentiable on \(\mathbb{R}^3_+ \setminus \mathcal{L}\).

As the proof of Proposition 2.2 and the completely analogous and therefore omitted proof of Proposition 5.1 show, assumption (B.III) is needed to show that \(\tilde{\beta}\) is a well-defined function of \(E\).
As in Section 2, the asymptotic dynamics of system (5.2) reduce in several cases to the asymptotic dynamics of

\[ y' = y\beta(y + az)\exp[-k(\beta(y + az))(y + az)] \]
\[ z' = m\mathcal{F}(1 - \exp[-k(\beta(y + az))az])y + \mathcal{F}z. \]

We have the following analog of Theorem 2.3.

**THEOREM 5.2**

Let the assumptions (B.I)-(B.III) hold, and assume that \( P = (x, y, z) \in \text{Int} \mathbb{R}^3 \) and \( M > \beta \). The triangle

\[ x + y + az = \frac{\log \beta}{k(\beta)}, \quad x \geq 0; \quad y \geq 0; \quad z \geq 0, \]  

contains one or two segments of nontrivial fixed points of (5.2). If the \( \omega \)-limit set \( \omega(P) \) of \( P \) is not a subset of the \( yz \) plane, then \( \omega(P) \) consists of a single point on one of the at most two segments with fixed points on the triangle (5.5). One has

\[ \frac{y'}{x'} \geq \frac{y}{x} \]  

and the exact location of \( \omega(P) \) depends on the initial state \( P \).

So, if \( M > \beta \) and the fixed points of (5.1) are unstable, the proportion of individuals using the adjustable strategy increases until a stable fixed point of system (5.2) is reached. If all the fixed points of system (5.2) are unstable, then the adjustable strategy outcompetes the fixed strategy. That is, when the adjustable strategy prevails, it stabilizes oscillating dynamics or outcompetes the fixed strategy.

In the next theorem we show that the adjustable strategy can stabilize oscillating dynamics in the case \( k(\beta) = \beta^p \).

**THEOREM 5.3**

Assume that \( k(\beta) = \beta^p \) and \( M > \beta \). Consider system (5.1) with \( p \) as bifurcation parameter, and assume that the fixed point in \( \text{Int} \mathbb{R}^2_+ \) loses its stability through a Hopf bifurcation as \( p \) decreases through \( p^* \). Then there exists an \( \varepsilon > 0 \) such that the fixed point in \( \text{Int} \mathbb{R}^2_+ \) of system (5.4) is locally asymptotically stable for \( p > p^* - \varepsilon \).

Theorem 5.3 states that for \( p \in [p^* - \varepsilon, p^*] \), the fixed point is unstable if the prey do not adjust their reproductive behavior to prey
and predator density, but stable if they do. Moreover, the adjustable strategy cannot be the reason for any observed oscillations. If the oscillations are present in the adjustable strategy case (5.4), they are also present in the fixed strategy case (5.1) for the corresponding parameter values.

6. NUMERICAL RESULTS

We supplement the analytical comparison of systems (5.1) and (5.4) in Sections 4 and 5 with a numerical study. Our aim is to make as complete a comparison as possible of systems (5.1) and (5.4) when $1 < \beta < M < \exp(2)$. Observe that this study includes a study of the system (3.2), (3.3).

We were interested in the case where $M$ was only slightly greater than $\beta$ and $k(\beta) = \beta^p$; that is, we compared the systems

$$\dot{X} = X \exp(1/p) \exp(-X - AX), \quad (6.1)$$
$$Z' = [1 - \exp(-AX)]X - FZ \quad (6.2)$$

and

$$Y' = \begin{cases} Y \exp\left(\frac{1}{p}\right) \exp(-Y - AX), & Y + AX < \frac{1 - \varepsilon}{p}, \\ Y \left(p(Y + AX)\right)^{-1/p}, & Y + AX > \frac{1 - \varepsilon}{p}, \end{cases} \quad (6.3)$$

$$Z' = \begin{cases} [1 - \exp(-AX)]Y + FZ, & Y + AX < \frac{1 - \varepsilon}{p}, \\ [1 - \exp\left(-\frac{AX}{p(Y + AX)}\right)]Y + FZ, & Y + AX > \frac{1 - \varepsilon}{p}, \end{cases} \quad (6.4)$$

with $X = k(\beta)x$, $Y = k(\beta)y$, $Z = k(\beta)z/(mF)$, $A = amF$, and $\varepsilon = 10^{-14}$. (The numerical accuracy in double precision is expected to be on the order of $10^{-15}$.)

We have used the approximations $M^p/\varepsilon \approx 1$ and $M \approx \exp(1/p)$ in (6.3), (6.4). The relative errors caused by these approximations are on the order of $10^{-14}$, so they are negligible compared to the relative errors in the calculation of $1 - \exp(-\xi)$ in (6.2) and (6.4). These errors
are on the order of $10^{-8} - 10^{-9}$, and they are of this order despite the fact that we used the formula

$$1 - \exp(-\xi) = \begin{cases} \xi, & 0 < \xi < \kappa, \\ 1 - \exp(-\xi), & \xi > \kappa. \end{cases} \quad (6.5)$$

A direct calculation of $1 - \exp(\xi)$ causes large cancellation errors for small $\xi$ on any computer, and this is usually followed by an unexpected extinction of the predator. In (6.5), $\kappa$ is a compiler- and precision-dependent constant. The optimal choices for $\kappa$ on our computers varied in the range $(0.37-0.94) \times 10^{-8}$ in double precision.

In Figure 2 we compare the solutions of systems (6.1), (6.2) (solid line) and (6.3), (6.4) (dotted line) in the case $\mathcal{A} = 3.0$ and $\mathcal{F} = 0.5$. The

![Figure 2](image.png)

**Fig. 2.** Comparison of system (6.1), (6.2) (solid line) and system (6.3), (6.4) (dotted line) in the case $\mathcal{A} = 3.0$ and $\mathcal{F} = 0.5$. (a) Amplitudes of the solutions. (b) The logarithm of the period. (c) The logarithm of the dominating period (the period corresponding to the maximum of the Fourier spectrum). (d) The Lyapunov exponent.
amplitude increases as a parabola for system (6.1), (6.2) [solid line, panel (a)], and faster than for system (6.3), (6.4) [dotted line, panel (a)]. System (6.3), (6.4) remains quasi-periodic after the Hopf bifurcation at \( \exp(1/p) = 3.90 \) [dotted line, panels (b) and (d)] as the parameter value \( \exp(1/p) \) (horizontal axis) is increased. Transition into periodic and chaotic behavior as the parameter value \( \exp(1/p) \) increases is observed for system (6.1)–(6.2) [solid line, panels (b) and (d)]. Some periodic solutions of (6.1), (6.2) are quite dominating—for example, the 19-periodic solution formed at \( \exp(1/p) = 5.80 \) and the 9-periodic solution near \( \exp(1/p) = \exp(2) \).

When the value of the parameter \( \mathcal{A} = am \mathcal{F} \) was increased, everything happened faster as expected from Theorem 4.1. In Figure 3 a

![Fig. 3. Comparison of system (6.1), (6.2) (solid line) and system (6.3), (6.4) (dotted line) in the case \( \mathcal{A} = 18.0 \) and \( \mathcal{F} = 0.5 \). (a) Amplitudes of the solutions. (b) The logarithm of the period. (c) The logarithm of the dominating period (the period corresponding to the maximum of the Fourier spectrum). (d) The Lyapunov exponent.](image-url)
comparison between the solutions of the systems (6.1), (6.2) (solid line) and (6.3), (6.4) (dotted line) in the case $\mathcal{A} = 18.0$ and $\mathcal{F} = 0.5$ is shown. Periodic or chaotic solutions started to appear also in model (6.3), (6.4). For system (6.1), (6.2), larger periodic windows are observed in the ranges $2.20 < \exp(1/p) < 2.67$ (period 44). A quite clear sequence of period doublings for system (6.3), (6.4) is observed at $\exp(1/p) = 6.98$ (a 16-periodic solution becomes 32-periodic) and $\exp(1/p) = 7.19$ (the 32-periodic solution becomes 64-periodic) [dotted line, Figure 3, panels (b) and (d)]. The dominant period [panel (c)] is almost constant regardless of period doublings and chaos.

When we decreased the value of $\mathcal{F}$, the Hopf bifurcation in systems (6.1), (6.2) and (6.3), (6.4) occurred later. This was not directly to be expected from Theorem 4.1. The reason for this is that the approximations used in the proof of Theorem 4.1 do not work well if $\mathcal{F}$ is small. In Figure 4 the solutions of system (6.1), (6.2) (solid line) and (6.3), (6.4) (dotted line) in the case $\mathcal{A} = 18.0$ and $\mathcal{F} = 0.1$ are compared. No chaotic solutions were detected for the system (6.3), (6.4) [dotted line, panel (d)]. The very dominating periodic window for system (6.3), (6.4) at $3.71088 < \exp(1/p) < \exp(2)$ has period 10. Also, system (6.1), (6.2) has a lot of periodic windows in the quasi-periodic regime, but a large 32-periodic window in the range $4.55 < \exp(1/p) < 5.63$ is very dominating. The oscillations of (6.1), (6.2) become chaotic for the first time when $\beta$ exceeds 6.16 here [solid line, panel (d)].

When we increased $\mathcal{A}$ enough, system (6.3), (6.4) started to possess chaotic solutions even if $\mathcal{F}$ was low. Figure 5 shows the situation in the case $\mathcal{A} = 21.0$ and $\mathcal{F} = 0.1$. The solution of (6.3), (6.4) becomes chaotic (after a clear period doubling $52-104-208\ldots$) for the first time when $\exp(1/p) = 4.97$, and the solution of (6.1), (6.2) becomes chaotic for the first time for $\beta = 5.81$. A quite dominant periodic solution of period 37 was observed in the range $4.054 < \exp(1/p) < 5.40$ for system (6.1), (6.2). Note that suppression of reproduction can cause transitions from periodic solutions or quasi-periodic solutions into chaotic solutions [panels (b)–(d)], but it will still have a stabilizing impact as measured by the mean amplitude [panel (a)] and the dominating period [panel (c)].

It is evident from these figures that suppression of reproduction generally decreases the amplitude of the oscillations and therefore has a global stabilizing effect. Another dominant feature in these results is that the adjustable strategy makes the dominating period shorter.

In Figure 6 are plotted the parameter values corresponding to nonperiodic behavior in the $(\mathcal{F}, \beta)$ parameter plane. Red is used to indicate chaotic behavior, blue to indicate quasi-periodic behavior, and no color to indicate periodic motion. The transition from regular behavior toward chaotic behavior does not occur along a well-defined
smooth curve in the parameter plane. This scenario is easier to follow in the case of system (6.3), (6.4), Figure 6b, because the resonance tongues are larger and correspond to lower periods. The transition involves multiple attractors, period doublings in the resonance tongues, and much more. For example, in the case of (6.3), (6.4), we found coexisting 10- and 11-periodic attractors at $\exp(1/p) = 7.33$ and $\mathcal{F} = 0.18$ (black circle, Figure 6b). In the case of (6.1), (6.2), the transition is more complete, and a region with almost only chaotic behavior can be discerned, cf. Figure 6a. The plot shows the situation for $\mathcal{F} = 18.0$.

The calculation of the Lyapunov exponent for system (6.3), (6.4) requires some explanation, as the system is not continuously differentiable. However, by Proposition 5.1(iii), the system is continuously...
differentiable almost everywhere, so in the case of quasi-periodic and complicated behavior, this discontinuity does not cause problems, because the Lyapunov exponent is a mean, and the contributions from the discontinuity points to this mean are not significant. Again, in the case of periodic behavior, a periodic solution does not generically lie on the discontinuity lines, so these contributions are essential in exceptional cases only. The assumption that $M > \beta$ guarantees that the fixed points do not lie on the discontinuity lines.

Our numerical results show that the discrete predator–prey model (3.2), (3.3) captures all the dynamics of related continuous predator–prey models with density-dependent prey growth such as the Gause-type predator–prey models and much more (cf. [13, 25–29]). The difference
between the discrete and the continuous case is here (as expected) as large as the famous difference between the discrete quadratic map and continuous logistic flow [13, 30].

7. DISCUSSION

We have presented several models describing intraspecific competition, predation, and adjustable reproductive behavior in the prey. Our models are hybrids between continuous- and discrete-time models. Quite realistically, reproduction has been modeled as occurring at discrete instants. On the other hand, predation is a continuous process occurring throughout the season, and consequently the effect of preda-
tion upon the population densities at the instants of reproduction has been obtained by integrating the corresponding continuous Lotka–Volterra system over the time between two reproductive events. In this paper we have chosen to model intraspecific competition using the familiar Ricker law. For a detailed description of the relation between the Ricker model and continuous intraspecific competition processes, we refer to [18].

Adaptive behavioral strategies generally have some costs associated with them that should be taken into account when considering the ultimate fitness payoff of the behavior. The adjustable reproductive behavior studied in this paper, reduced clutch size under certain conditions, does not appear to entail any such costs. On the contrary, resources not used for reproduction should remain available for other functions. An interesting additional question about the adjustments is whether they might occur with a time delay, which would have potentially destabilizing consequences. Though such time delays are possible, they are unlikely to occur in the case of the empirical example considered in this paper—rodents exposed to intraspecific competition and predation. Breeding females are able to fine-tune their reproductive effort by resorbing embryos and possibly by selectively lactating only some of their offspring.

We assumed a specific functional form for the trade-off between the reproductive effort and competitive ability, such as is predicted by the life history theory and is empirically observed for a range of organisms [16]. In this case, selection will maximize the equilibrium population size. We have rigorously proved for the model analyzed here that the equilibrium population size will be maximized regardless of its stability. Hence, selection will not eliminate complex dynamics associated with an unstable equilibrium. For some parameter values, the winning type shows chaotic dynamics. Similar results have been obtained with other models [31].

The Ricker model has the property that the nontrivial equilibrium equals the average population size even in the case of chaotic dynamics. Thus the result mentioned above can be reformulated by saying that selection maximizes mean population size, a result that is well known from previous work [32]. This is an important observation, because in [18] we showed that if intraspecific competition is modeled as a continuous process during the season, then it may very well happen that the winning type has lower equilibrium density, whereas it is still true it has higher mean density. Thus even if the assumptions of continuous and discrete intraspecific competition lead to different models, both models share the property that they predict that selection maximizes mean population size.
The key result for the models analyzed in this paper is generally stabilizing effect of optimal reproductive adjustments. In the single-species competition model this stabilizing effect is apparent in reduced mean amplitude of population oscillations. In the predator–prey model, optimal reproductive behavior of the prey may have a more striking effect, by transforming a periodic solution to a fixed point. Chaotic dynamics may become transformed to periodic or quasi-periodic dynamics by optimal reproductive suppression, but the reverse may also occur (Figures 5 and 6), though in all cases stability as measured by the mean amplitude is increased. In the case of pure predator–prey oscillations (cf. Section 3), our numerical results demonstrated a decrease in the dominant period of oscillations in the presence of adjustable reproductive behavior.

It is in general difficult to determine periods and Lyapunov exponents from short and noisy empirical time series, and our results show that optimal adjustment of reproduction does not affect these quantities in a clear-cut way. Regardless of the dynamics, dominating periods and mean amplitudes are easy to determine from observations, and these quantities are expected to be negatively correlated to optimal adjustment of reproduction.

Prey types capable of optimally suppressing their reproduction generally outcompete types that lack such flexibility, and this will generally increase stability, but the Lyapunov exponent of the dynamics of the winning type may be less or greater than the Lyapunov exponent of the other types.

The empirical results for microtine rodents from Fennoscandia suggest that suppression of reproduction is stronger in the northern populations with a fairly regular high-amplitude cycle than in the more stable southern populations [3]. This observation is consistent with the present results: Reproductive adjustment is not expected when the equilibrium point is stable, because then nothing is to be gained by delaying reproduction. Our results suggest that the observed behavioral responses of voles to risk of predation in the high-amplitude northern populations are not the cause of the oscillations, but in contrast the oscillations occur in spite of the potentially stabilizing behavioral responses.

8. PROOFS

If a map \( w \rightarrow w' \) is defined in \( \mathbb{R}^k \), then the (forward) orbit of \( w_0 \) obtained by iterating the map starting at \( w_0 \) is denoted by \( \{w_n\}^\infty_{n=0} \). The components are indexed correspondingly—for example, \( w_n = (x_n, y_n) \) for orbits in \( \mathbb{R}^2 \).
Proof of Proposition 2.1. We first notice that it follows from our assumptions that every orbit is bounded. Next observe that
\[
\frac{(x')^{1/k_1}}{(y')^{1/k_2}} = \frac{\beta_1^{1/k_1} \exp(-E) x^{1/k_1}}{\beta_2^{1/k_2} \exp(-E) y^{1/k_2}} = \frac{\beta_1^{1/k_1}}{\beta_2^{1/k_2}} \left( \frac{x^{1/k_1}}{y^{1/k_2}} \right).
\]
If \( x^* > y^* \), that is, if \( \log \beta_1 / k_1 > \log \beta_2 / k_2 \), then \( x_n^{1/k_1} / y_n^{1/k_2} \) tends to infinity in a geometrical progression as \( n \) tends to infinity. Since all orbits are bounded, this is possible only if \( y_n \) tends to zero. The conclusion for the reverse inequality is proved in an identical way.

Proof of Proposition 2.2. For every \( E \in \mathbb{R}_+ \), the continuous function
\[
\psi_E(\beta) := \beta \exp[-k(\beta)E]
\]
attains its maximum in the compact interval \((0, M)\). As \( \psi_E \) is positive and \( \psi_E(0) = 0 \), the maximum is in fact attained in \((0, M)\). If it is attained at \( \beta \in (0, M) \), then
\[
\psi'_E(\beta) = [1 - \beta k'(\beta)E] \exp[-k(\beta)E] = 0.
\]
Equation (8.1) holds if and only if
\[
\chi(\beta) := \frac{1}{\beta k'(\beta)} = E.
\]
It follows from (B.III) that \( \chi \) is strictly decreasing on \((0, \infty)\) and hence Equation (8.2) can have at most one solution in \((0, M)\). This proves (i).

If \( E \leq 1/Mk'(M) \), then Equation (8.2) has no roots in \((0, M)\), and hence \( \psi_E \) attains its maximum at the endpoint \( \beta = M \). If this is not the case, then by (i) the maximum is attained in \((0, M)\). It follows in particular that \( \lim_{\beta \to 0^+} \chi(\beta) = \infty \). Thus,
\[
\tilde{\beta}(E) = \begin{cases} M & \text{if } 0 \leq E \leq 1/Mk'(M), \\ \chi^{-1}(E) & \text{if } 1/Mk'(M) < E < \infty. \end{cases}
\]
All the assertions of (ii) except formula (2.8) follow from (8.3). But by (B.II), \( \tilde{\beta} \) is the unique zero of the derivative of the function \( \beta \mapsto \log(\beta)/k(\beta) \) and using this fact one easily shows that (2.8) holds.

Finally we note that the \( \chi^{-1} \) is continuously differentiable and hence \( \tilde{\beta} \) is continuously differentiable except possibly at \( E = M \) by (8.3). This proves (iii).
Proof of Theorem 2.3. The inequality (2.10) follows immediately because $0 < \hat{\beta} < M$. If $y_n / x_n \to \infty$, then the $\omega$-limit set is a subset of the $y$ axis because every orbit is bounded. On the other hand, if $y_n / x_n$ tends to a positive real value $C$, then

$$\hat{\beta}(x + y) = \hat{\beta}$$

and

$$y = Cx$$

for all $(x, y) \in \omega(P)$. By (8.4) and Proposition 2.2(ii), we have

$$0 < x + y < \log(\hat{\beta}) / k(\hat{\beta})$$

for all $(x, y) \in \omega(P)$. [The latter inequality in (8.6) is an equality if $\hat{\beta} < M$.]

It follows from (8.4) that we can add the two first equations in model (2.7) (this operation is valid in the corresponding $\omega$-limit set) and arrive at

$$(x + y)' = \hat{\beta}(x + y)\exp\left[-k(\hat{\beta})(x + y)\right].$$

The map (8.7) is equivalent to the map (2.11), so the only subset of the domain defined by (8.6) that can be an $\omega$-limit set is the segment

$$x + y = \log(\hat{\beta}) / k(\hat{\beta}).$$

Thus every point in $\omega(P)$ satisfies both (8.5) and (8.8), and thus $\omega(P)$ consists precisely of the unique point of intersection between the straight lines (8.5) and (8.8).  

Proof of Theorem 4.1. To facilitate the analysis we perform the linear change of variables

$$x' = k(\beta)x,$$

$$x = [k(\beta) / mF]z$$

and introduce the new parameters

$$\mathcal{A} = amF,$$

$$\mathcal{B} = 1 - \mathcal{A}.$$
Equations (3.2) and (3.3) then take the form

\[
\frac{\mathcal{X}'}{\mathcal{Y}} = \mathcal{X} \exp(-\mathcal{A} - \mathcal{X}), \quad (8.13)
\]

\[
\frac{\mathcal{Y}'}{\mathcal{X}} = \left[1 - \exp(-\mathcal{A} \mathcal{X})\right] \mathcal{X} + \mathcal{Y}. \quad (8.14)
\]

We calculate the location of the interior fixed points, if some exist. From the prey equation we get

\[
\log \beta = \mathcal{X} + \mathcal{A} \mathcal{X}, \quad (8.15)
\]

and from the predator equation we get

\[
\frac{\mathcal{Y}}{\mathcal{X}} = 1 - \exp(-\mathcal{A} \mathcal{X}). \quad (8.16)
\]

One can show that system (8.15), (8.16) has a unique solution ($\mathcal{X}^*, \mathcal{Y}^*$) [except the solution ($\log(\beta), 0$)] and that the solution of (8.16) defines a concave function $\mathcal{Y} = \mathcal{Y}(\mathcal{X})$. It is important to note that the solution of system (8.15), (8.16) satisfies $\mathcal{X}^* < \log(\beta) < 2$, $\mathcal{D}/\mathcal{A} < \mathcal{X}^*$ [put $\mathcal{A} \mathcal{X}^* > 1 - \exp(-\mathcal{A} \mathcal{X}^*)$ in (8.16)], $\mathcal{X}^*/\mathcal{A} > \mathcal{X}^*$ [put $1 > 1 - \exp(-\mathcal{A} \mathcal{X}^*)$ in (8.16)], and $\mathcal{X}^* > (\mathcal{X}^* - \mathcal{D}/\mathcal{A})/\mathcal{D}$ [the estimate

\[
1 - \exp(-\mathcal{A} \mathcal{X}) > \frac{\mathcal{X}}{1 + \mathcal{X}}
\]

can be substituted in (8.16)]. As these inequalities are important and will be used later, we give names to them according to

\[
\frac{\mathcal{D}}{\mathcal{A}} < \mathcal{X}^* < 2, \quad (8.17)
\]

\[
\frac{\mathcal{X}^* - 1}{\mathcal{D}} < \mathcal{X}^* < \frac{\mathcal{X}^*}{\mathcal{D}}. \quad (8.18)
\]

The characteristic equation of the Jacobian of system (8.14) calculated at the unique fixed point ($\mathcal{X}^*, \mathcal{Y}^*$) in the interior of the state space is a quadratic equation. Denote the coefficients by $p$ and $q$, as in $\lambda^2 + p\lambda + q = 0$. We shall then prove that $-1 + |p| < q < 1$ when $0 < \mathcal{A} < \mathcal{I}$ and $-1 + |p| < q$ when $\mathcal{A} > \mathcal{I}$. As ($\mathcal{X}^*, \mathcal{Y}^*$) can lose its stability only if $\lambda_1\lambda_2 = 1$, and at least one eigenvalue has to have modulus 1 in a bifurcation point, both eigenvalues have to be either 1 or $-1$ if they are real.
We proceed by calculating the Jacobian of system (8.14) in \((x^*, z^*)\) and arrive at
\[
J(x^*, z^*) = \begin{pmatrix}
1 - z^* & -x^* \\
\frac{D_z^*}{z^*} & x^- \left(1 - \frac{D_z^*}{z^*}\right)
\end{pmatrix}.
\]

The characteristic polynomial is given by
\[
\lambda^2 - \text{Tr} J(x^*, z^*) \lambda + \text{det} J(x^*, z^*),
\]
so we have to require
\[
-1 - \text{Tr} J(x^*, z^*) < \text{det} J(x^*, z^*), \quad (8.19)
\]
\[
-1 + \text{Tr} J(x^*, z^*) < \text{det} J(x^*, z^*), \quad (8.20)
\]
\[
\text{det} J(x^*, z^*) < 1, \quad (8.21)
\]
for local stability. We have
\[
\text{Tr} J(x^*, z^*) = 1 - x^* + x^- z^* - x^- z^* + I, \quad (8.22)
\]
\[
\text{det} J(x^*, z^*) = x^* - x^* z^* + I - x^* z^* + x^* z^* - x^* z^*. \quad (8.23)
\]

We start by proving inequality (8.19). We substitute expressions (8.22) and (8.23) and get
\[
-1 - 1 + x^* - x^* - x^* z^* - I < x^* - x^* z^* + I - x^* z^* + x^* z^* - x^* z^* < 0.
\]
\[
(8.24)
\]

Inequality (8.24) is equivalent to
\[
-2 - 2I + x^* - 2x^* + I - x^* z^* + x^* z^* - x^* z^* < 0.
\]
\[
(8.25)
\]

We show first that (8.25) holds if \(x^* > 1\). We show this by the following series of inequalities.
\[
-2 - 2I + x^* - 2x^* + I - x^* z^* + x^* z^* - x^* z^* < \max(-1 - I, 0) + (1 - x^*) I - x^* z^* < 0.
\]
\[
(8.26)
\]

The first inequality in (8.26) holds because \(-2 - 2I + x^* - 2x^* + I - x^* z^* + x^* z^* - x^* z^*\) is a convex function of \(x^*\) and \(1 < x^* < \log(\beta) < 2\).
If $0 < \varepsilon^* < 1$, we show that the inequality (8.25) holds by the following series of inequalities

\[-2 - 2I + X^* - 2AX^* + XX^* + ADX^* - AX^*D^{-1}X^* \leq -2 - 2I + X^* - 2AX^* + XX^* + ADX^* - AX^*D^{-1}X^* \leq -2 - 2I + X^* - AX^* + XX^* \leq \max(-2 - 2I, -1 - I - A) < 0. \quad (8.27)\]

The first inequality in (8.27) holds because $X^* < X^*/D$.

We continue with inequality (8.20). We substitute (8.22) and (8.23) and get

\[-1 + 1 - X^* + AX^* - ADX^* + I < AX^* + I - AX^* + AX^*D^{-1}X^* - X^* + DX^*. \quad (8.28)\]

Inequality (8.28) is equivalent to

\[-ADX^* + AX^* + ADX^* - DX^* < 0. \quad (8.29)\]

We prove that (8.29) holds using that $X^* > X^*/D - 1/A$, cf. (8.18). We get

\[-ADX^* + AX^* + ADX^* - DX^* \leq \quad \leq -AD(1)(X^* + 1)\left(\frac{D}{D} - \frac{1}{A}\right) + AX^* + ADX^* - DX^* \leq \quad \leq -AX^* + DX^* - AX^* + D + AX^* + D - DX^* \leq \quad \leq -AX^* + D < 0. \quad (8.30)\]

The last inequality in (8.30) holds because $X^* > D/A$, cf. (8.17).

Finally, we want to find conditions implying (8.21), that is,

\[AX^* - D - AX^2 + AX^*D^{-1}X^* - XX^* < 0\]

or

\[X^* < \frac{1}{AX^*} - \frac{1}{D} + \frac{I}{AD} + \frac{XX^*}{D} = F(X^*).\]
The function $F(x^*)$ is convex and the curve determined by (8.16) was concave; hence they can intersect at most twice. If $0 < \alpha < \mathcal{F}$, they do not intersect at all because

$$F(x^*) = \frac{1}{x^*} + \frac{\mathcal{F} - \alpha}{\mathcal{B}} + \frac{x^*}{\mathcal{B}} > \frac{x^*}{\mathcal{B}}.$$ 

Again, if $\alpha > \mathcal{F}$, these curves intersect once, because of their asymptotic behavior. They intersect in the fixed point $(x^*, z^*)$, corresponding to the parameter value $\beta^*$, and the theorem follows.

**Proof of Theorem 5.2.** Because $M > \beta$ we get

$$\frac{y'}{x} \geq \frac{y}{x}.$$ 

If $y_n/x_n \to \infty$, then the $\omega$-limit set is a subset of the $yz$ plane, because every orbit is bounded. Again, if $y_n/x_n$ tends to some nonnegative real value, then we have $\beta = \beta$, $y/x = C$, and $0 < C < \infty$ in $\omega(P)$. By Proposition 5.1(ii) we get $x + y + az = \log(\hat{\beta})/k(\hat{\beta})$ in $\omega(P)$, so $\omega(P)$ is a subset of the solution to

$$y/x = C, \quad 0 < C < \infty,$$

$$x + y + az = \log(\hat{\beta})/k(\hat{\beta}),$$

which is a straight line in $\mathbb{R}^3$. As system (5.2) restricted to this line is equivalent to system (3.2), (3.3), we conclude that all the points except the fixed points on this line, are mapped to points outside this line; cf. the beginning of the proof of Theorem 4.1. Hence, $\omega(P)$ consists of a single point.

**Proof of Theorem 5.3.** We start by performing the transformations $\zeta = z/m\mathcal{F}$ and $\alpha = am\mathcal{F}$ in systems (5.1) and (5.4), respectively. We get

$$x' = x\hat{\beta} \exp[-k(\hat{\beta})(x + \alpha\zeta)],$$

$$\zeta' = \left(1 - \exp[-k(\hat{\beta})\alpha\zeta]\right)x + \mathcal{F}\zeta$$

and

$$y' = y\hat{\beta} \exp[-k(\hat{\beta})(y + \alpha\zeta)],$$

$$\zeta' = \left(1 - \exp[-k(\hat{\beta})\alpha\zeta]\right)y + \mathcal{F}\zeta,$$
respectively, where $\hat{\beta}$ is as defined by (5.3). Using the fact that $k(\beta) = \beta^p$, we observe that $\hat{\beta} = \exp(1/p)$. The map corresponding to (8.32) is therefore given by

$$
x' = x \exp(1/p) \exp[ - e(x + \mathcal{A} \zeta) ],
$$
$$
\zeta' = [1 - \exp(-e\mathcal{A} \zeta)] x + \mathcal{F} \zeta,
$$

(8.34)

and the map corresponding to (8.33) is given by

$$
y' = \begin{cases} 
y M \exp[ - M^p (y + \mathcal{A} \zeta) ], & y + \mathcal{A} \zeta < 1/pM^p, \\
y [p e(y + \mathcal{A} \zeta)]^{-1/p}, & y + \mathcal{A} \zeta > 1/pM^p,
\end{cases}
$$

(8.35a)

$$
\zeta' = \begin{cases} 
[1 - \exp(-M^p \mathcal{A} \zeta)] y + \mathcal{F} \zeta, & y + \mathcal{A} \zeta < 1/pM^p, \\
[1 - \exp\left(-\frac{\mathcal{A} \zeta}{p(y + \mathcal{A} \zeta)}\right)] y + \mathcal{F} \zeta, & y + \mathcal{A} \zeta > 1/pM^p,
\end{cases}
$$

(8.35b)

Using the new coordinates $\zeta = e^x$, $\mathcal{X} = e^x$, and $\mathcal{A} = ey$, respectively, we can simplify Equations (8.34) and (8.35) to

$$
\mathcal{X}' = \mathcal{X} \exp(1/p) \exp(- \mathcal{X} - \mathcal{A} \mathcal{Z}),
$$

$$
\mathcal{Z}' = [1 - \exp(-\mathcal{A} \mathcal{Z})] \mathcal{X} + \mathcal{F} \mathcal{Z},
$$

(8.36)

and

$$
\mathcal{X}' = \begin{cases} 
\mathcal{X} M \exp\left(-\frac{M^p \mathcal{A} \zeta}{e(y + \mathcal{A} \zeta)}\right), & \mathcal{X} + \mathcal{A} \zeta < \frac{e}{pM^p}, \\
\mathcal{X} \left[p(\mathcal{X} + \mathcal{A} \zeta)\right]^{-1/p}, & \mathcal{X} + \mathcal{A} \zeta > \frac{e}{pM^p},
\end{cases}
$$

(8.37a)

$$
\mathcal{Z}' = \begin{cases} 
[1 - \exp\left(-\frac{M^p \mathcal{A} \zeta}{e(\mathcal{X} + \mathcal{A} \zeta)}\right)] \mathcal{X} + \mathcal{F} \mathcal{Z}, & \mathcal{X} + \mathcal{A} \zeta < \frac{e}{pM^p}, \\
[1 - \exp\left(-\frac{\mathcal{A} \zeta}{p(\mathcal{X} + \mathcal{A} \zeta)}\right)] \mathcal{X} + \mathcal{F} \mathcal{Z}, & \mathcal{X} + \mathcal{A} \zeta > \frac{e}{pM^p}.
\end{cases}
$$

(8.37b)

Because $M > \exp(1/p)$, we have to compare the stability properties of the map

$$
\mathcal{X}' = \mathcal{X} \left[p(\mathcal{X} + \mathcal{A} \zeta)\right]^{-1/p},
$$

(8.38a)

$$
\mathcal{Z}' = [1 - \exp\left(-\frac{\mathcal{A} \zeta}{p(\mathcal{X} + \mathcal{A} \zeta)}\right)] \mathcal{X} + \mathcal{F} \mathcal{Z}
$$

(8.38b)
with stability properties of the map (8.36) (compare the proof of Theorem 4.1).

Note that \((x^*, z^*)\) satisfies
\[
x^* + s x^* = 1/p,
\]
\[
s x^* / x^* = 1 - \exp(-sx^*).
\]

Let \(J^*(x^*, z^*)\) be the Jacobian of system (8.38) calculated at \((x^*, z^*)\). We get
\[
J^*(x^*, z^*) = \begin{pmatrix} 1 - x^* & -sx^* \\ \frac{dx^*}{dx^*} - p x^* z^* + p D z^2 & s x^* + p D x^* + I \end{pmatrix}.
\]

We have
\[
\text{Tr} J^*(x^*, z^*) = 1 - x^* + I + s x^2 - p D x^* z^*, \quad (8.39)
\]
\[
\det J^*(x^*, z^*) = s x^2 - p D x^* z^* + I - s x^2
+ s D x^* z^* - R x^* + s D z^*. \quad (8.40)
\]

To complete the proof we have to show that
\[
-1 - \text{Tr} J^*(x^*, z^*) < \det J^*(x^*, z^*), \quad (8.41)
\]
\[
-1 + \text{Tr} J^*(x^*, z^*) < \det J(x^*, z^*), \quad (8.42)
\]
\[
\det J^*(x^*, z^*) < \det J(x^*, z^*). \quad (8.43)
\]

We prove first that (8.41) holds. We substitute (8.39) and (8.40) and arrive at
\[
-2 + x^* - 2I - 2s x^2 + 2s D x^2 z^* + s x^2 - p D x^* z^*
+ R x^* - D A z < 0. \quad (8.44)
\]

Inequality (8.44) holds because of the following series of inequalities.
\[
-2 + x^* - 2I - 2s x^2 + 2s D x^2 z^* + s x^2 - D A x^* z^* + R x^* - D A z
= -2 + x^* - 2I - 2s x^2 + 2s D x^2 z^* + R x^* - D A z + D A x^* (2p - 1) z^*
\[
< -2 + x^* - 2I - 2s x^2 + 2s D x^2 z^* + R x^* - D A z + s x^2 (2p - 1)
\[
= -2 + x^* - 2I + R x^* - D A z^*
\[
< \min(-2 - 2I, 0) - D A z^* < 0.
\]
We assumed basically that $0 < \frac{D}{A} \cdot A < A^* < 1/p < 2$ and $Z^* < Z^*/D$. To prove (8.42) we show that

$$AX^* - \frac{D}{p} - ADX^* < 0. \quad (8.45)$$

Inequality (8.45) holds because of the following series of inequalities.

$$AX^* - \frac{D}{A} - DZ^* - ADZ^* \quad < \quad AX^* - \frac{D}{A} - DZ^* - ADZ^* \left( \frac{Z^*}{D} - \frac{1}{A} \right) \quad = \quad AX^* - \frac{D}{A} - DZ^* - ADZ^* + DZ^* = -DZ^* < 0.$$ 

Finally, we substitute (8.23) and (8.40) in (8.43) and get

$$AX^* - ADX^* + AZ^* - AX^* < 0. \quad (8.46)$$

Inequality (8.46) holds because of the following series of inequalities.

$$AX^* - ADX^* + AZ^* - AX^* \quad = \quad AX^* + AZ^* p \left( \frac{1}{p} - Z^* \right) - AX^* \quad < \quad AX^* + AZ^* p \left( \frac{1}{p} - Z^* \right) - AX^* = 0.$$ 

We have used the estimates $1/p > Z^*$ and $Z^* < Z^*/d$ here. The proof is complete.

Remark 8.1. Note that system (8.38) is not a reasonable predator–prey model in the state space $R^2$, because the net reproduction number of the prey ($Z^*$) tends to infinity as both the prey and predator densities tend to zero. System (8.38) is used solely as a tool in the proof of Theorem 5.3 and lacks biological interpretation.

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