

Qualitative analysis of a predator-prey system with limit cycles

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Abstract. Fairly regular multiannual microtine rodent cycles are observed in boreal Fennoscandia. In the southern parts of Fennoscandia these multiannual cycles are not observed. It has been proposed that these cycles may be stabilized by generalist predation in the south.

We show that if the half-saturation of the generalist predators is high compared to the number of small rodents the cycles are likely to be stabilized by generalist predation as observed. We give examples showing that if the half-saturation of the generalist predators is low compared to the number of small rodents, then multiple equilibria and multiple limit cycles may occur as the generalist predator density increases.

Key words: Predator-prey system – Limit cycle – Hopf-bifurcation – Specialist predator – Generalist predator

1 Introduction

Fairly regular multiannual microtine rodent cycles are observed in boreal Fennoscandia. In the southern parts of Fennoscandia these multiannual cycles are not observed. The quite regular cycles in boreal Fennoscandia have been the object of extensive research, and a number of attempts have been made to explain the cycles, see [5, 7, 15, 23, 25].

May [23] suggested that the delay-differential equation

$$\dot{N} = rN(t)(1 - N(t - T)/K) \quad (1.1)$$

may describe the above mentioned phenomenon. Here N is the small rodent population, T is a time-lag and K is the environmental carrying capacity. Furthermore he showed that a time lag of about 8–9 months could generate a 3–4 year cycle. It is an interesting fact that the time between the summers in the boreal regions is approximately 8–9 months but this does still not explain how such a time-lag would ensue.

Hörnfeldt [7] studied other species interacting with the rodent cycle, in particular Tengmalm's owl, an avian vole-eating predator. Several mechanisms which could generate the time-lag in the model (1.1) were also proposed in [7].

Among them are predator-based, food-based and disease-based mechanisms. However, none of these hypotheses have yet been supported by enough data.

Some attempts have also been made to explain why the cycles are not observed in the southern parts of Fennoscandia, see e.g. [4, 5]. One explanation is that the small rodent populations are exposed to different kinds of predation in different parts of Fennoscandia. Hanski et al. [4] proposed the models

$$\begin{aligned}\dot{s} &= rs(1 - s/K) - cx \frac{s}{s + a_1} - ys^2 \\ \dot{x} &= qx(1 - x/\gamma s),\end{aligned}\tag{1.2}$$

and

$$\begin{aligned}\dot{s} &= rs(1 - s/K) - cx \frac{s}{s + a_1} - y \frac{s^2}{s^2 + b_2} \\ \dot{x} &= qx(1 - x/\gamma s)\end{aligned}\tag{1.3}$$

to explain the geographic variations. Here s is the small rodent density, x the specialist predator density and y is the generalist predator density. Note that y is not a dynamical variable but only a parameter. The growth rate of the prey is logistic with carrying capacity K and intrinsic growth rate r . The functional response (trophic function) of the specialist predators is Holling II (Michaelis–Menten kinetics) with half-saturation a_1 and the functional response of the generalist predators is Holling III with half-saturation $\sqrt{b_2}$, cf. [23]. The models (1.2) and (1.3) contain two kinds of predation, specialist predation and generalist predation and the environmental carrying capacity for the specialist predator is directly proportional to the prey density, cf. [22, 24].

Hanski et al. [4] also showed by simulation techniques that generalist predation is likely to be the main stabilizing factor in the south. In the models (1.2) and (1.3) it is assumed that the microtine rodent cycles are pure predator-prey cycles, not cycles generated by a time-lag as in the model (1.1), which cause the specialist predators to follow the cycle, cf. [7].

Models like (1.2) and (1.3) are predator-prey models. Predator-prey models have together with their higher dimensional generalizations (competition models, food chains and cooperation models) attracted quite much mathematical interest during the last decades (especially competition models) see e.g. [1, 2, 8, 9, 14, 17].

Although the higher dimensional models seem to have attracted more attention mainly due to their rich variety of phenomena (chaos, complicated bifurcations and so on) there are still unsolved two-dimensional problems. For example there are still only a few quite rough methods of general validity when one starts to investigate the simplest nonlinear phenomenon, limit cycles, cf. [28].

The models (1.2) and (1.3) differ from the mathematically most well-known predator-prey systems in the quite special predator equation. Usually the predator growth equation is of the form

$$\dot{x} = \left(m \frac{s}{s + a} - d \right) x,$$

i.e. biomass is transferred from the prey population to the predator population.

In this paper we shall give a qualitative analysis of a single predator-prey model containing the models (1.2) and (1.3) as special cases. We shall analyze the number and stability of the equilibria and, existence and location of limit cycles. The main mathematical methods are the Poincaré–Bendixson theorem,

Lyapunov functions, the Hopf-bifurcation stability formula (cf. [3]) and the theory of general rotated vector fields (cf. [28]). The results are summarized at the end of the paper.

2 The model

We generalize the models introduced in [4] to the following

$$\begin{aligned} \dot{s} &= h(s) - xf(s) - yf_g(s) \\ \dot{x} &= x\vartheta(x/s). \end{aligned} \tag{2.1}$$

This model contains the models (1.2) and (1.3) as two important special cases. We shall analyze the model (2.1) qualitatively under the following general conditions:

- (A-I) All the functions h, f, f_g and ϑ are continuously differentiable of any required order (At least C^1).
- (A-II) The function h satisfies $h(s) > 0$ if $0 < s < K$ and $h(s) < 0$ if $s < 0$ or $s > K$.
- (A-III) The functions f and f_g are increasing and have unique zeros at $s = 0$.
- (A-IV) The function ϑ is decreasing and satisfies $0 < \vartheta(t) < \infty$ if $0 \geq t < \kappa$ and $\vartheta(t) < 0$ if $t > \kappa$.
- (A-V) The function $\Psi(s)$ defined by

$$\Psi(s) = \int_A^s \frac{\vartheta(\kappa A/s')}{f(s')} ds' \tag{2.2}$$

satisfies $\lim_{s \rightarrow 0} \Psi(s) = \infty$ and $\lim_{s \rightarrow \infty} \Psi(s) = \infty, \forall A \in \mathbf{R}_+$.

Example 2.1 The systems (1.2) and (1.3) clearly satisfy the conditions (A-I)–(A-IV). Moreover, the condition (A-V) is also satisfied because

$$\int_A^s \frac{q}{c} \frac{1 - A/\tilde{s}}{\tilde{s} + a_1} d\tilde{s} = \frac{q}{c} \int_A^s \left(1 + (a_1 - A) \frac{1}{\tilde{s}} - Aa_1 \frac{1}{\tilde{s}^2} \right) d\tilde{s}, \tag{2.3}$$

which diverges in the required sense.

The system (2.1) may be written in the following form

$$\begin{aligned} \dot{s} &= f(s)(F_y(s) - x) \\ \dot{x} &= x\vartheta(x/s) \end{aligned} \tag{2.4}$$

which is more suitable for two dimensional phase-plane analysis. The function $F_y(s)$ is defined by

$$F_y(s) = \frac{h(s) - yf_g(s)}{f(s)}. \tag{2.5}$$

We shall also need a function $G(s)$ defined by

$$G(s) = \frac{f_g(s)}{f(s)}. \tag{2.6}$$

Remark 2.2 Most of the analysis in this paper is with small modifications also valid for the more general predator-prey system

$$\begin{aligned} \dot{s} &= f(s)(F_y(s) - \pi(x)) \\ \dot{x} &= \varrho(x)\vartheta(x/s) \end{aligned} \tag{2.7}$$

where π and ϱ are supposed to be increasing functions with unique zeros at zero. Note, however, that especially the proof of Theorem 6.4 does not (at least not immediately) carry over.

Theorem 2.3 *Assume (A-I)–(A-V). If $s(0) > 0$, $x(0) > 0$ and*

$$\lim_{s \rightarrow 0} F_y(s) > 0 \tag{2.8}$$

then the solutions $s(t)$ and $x(t)$ of (2.4) remain positive and bounded.

Proof. (a) Assume first $\lim_{s \rightarrow 0} F_y(s) = \infty$. The solutions will never cross the x -axis because we have $\dot{s} > 0$ close to the x -axis. Hence $s(t) > 0$. The s -axis consists of different trajectories of the system, and hence, we have $s(t) > 0$ by uniqueness of solutions.

(b) Assume now $\lim_{s \rightarrow 0} F_y(s) = F_y(0) < \infty$. Put

$$\begin{aligned} \underline{x} &= \inf\{F_y(s) \mid F_y(s) > \kappa s\} \\ \mathcal{A} &= \{(s, x) \mid 0 < s < \underline{x}/\kappa, x > \underline{x}\}. \end{aligned}$$

We introduce the Lyapunov level curves

$$V(s, x) = \int_{\underline{x}/\kappa}^s \frac{\vartheta(\underline{x}/s')}{f(s')} ds' + \int_x^{\underline{x}} \frac{x' - \underline{x}}{x'} dx', \tag{2.9}$$

in the region \mathcal{A} and note that

$$\begin{aligned} \dot{V} &= \vartheta(\underline{x}/s)(F_y(s) - x) - \vartheta(x/s)(\underline{x} - x) \\ &= \vartheta(\underline{x}/s)(F_y(s) - x) - \vartheta(\underline{x}/s)(\underline{x} - x) \\ &\quad + \vartheta(\underline{x}/s)(\underline{x} - x) - \vartheta(x/s)(\underline{x} - x) \\ &= \vartheta(\underline{x}/s)(F_y(s) - \underline{x}) + (\vartheta(\underline{x}/s) - \vartheta(x/s))(\underline{x} - x) \leq 0, \end{aligned}$$

whenever $(s, x) \in \mathcal{A}$. That is, wherever the trajectory starts or enters the region \mathcal{A} it cannot pass the x -axis at the boundary of \mathcal{A} . The rest of the proof of positivity is analogous to part (a).

(c) To prove dissipativity we note that all solutions will enter the rectangular region determined by $0 < s < K$ and $0 < x < K\kappa$. \square

Remark 2.4 The condition (2.8) states that generalist predators hunt alternative prey when the prey population is sufficiently small.

3 Equilibria and their stability

In this section we shall do some local equilibria analysis. We have equilibria at the solutions of the equations

$$\begin{aligned} h(s) - yf_g(s) &= 0 \\ x &= 0 \end{aligned} \tag{3.1}$$

and

$$\begin{aligned} x &= \kappa s \\ F_y(s) &= \kappa s. \end{aligned} \tag{3.2}$$

Equilibria lying in the interior of \mathbf{R}_+^2 are called interior equilibria. Since an infinite number of fixed points in a dissipative system can be removed by an arbitrary small perturbation we can assume that the number of fixed points is finite and introduce the following notation.

Notation 3.1 We denote the solutions of $h(s) - yf_g(s) = 0$ in descending order by $K_1, K_2, K_3, \dots, K_m$.

Notation 3.2 We denote the solutions of (3.2) in descending order by $(s_1^*, x_1^*), (s_2^*, x_2^*), \dots, (s_n^*, x_n^*)$. If it is clear from the context, which solution of (3.2) is under consideration we shall denote it by (s^*, x^*) .

The equilibria at $(0, K_i)$ are saddle points if $F'_y(K_i) < 0$ and unstable nodes if $F'_y(K_i) > 0$. We shall treat the origin as a saddle point when $\lim_{s \rightarrow 0} F_y(s) > 0$. The following theorem characterizes the interior equilibria.

Theorem 3.3 Assume (A-I)–(A-V).

(a) If $F'_y(s_i^*) - \kappa < 0$ then the equilibrium at (s_i^*, x_i^*) is not a saddle point. On the other hand, if $F'_y(s_i^*) - \kappa > 0$ then the equilibrium at (s_i^*, x_i^*) is a saddle point.

(b) If the equilibrium at (s_i^*, x_i^*) is not a saddle point then the expression

$$f(s_i^*)F'_y(s_i^*) + \kappa\vartheta'(\kappa) \tag{3.3}$$

determine the stability of the equilibria as follows:

If $f(s_i^*)F'_y(s_i^*) + \kappa\vartheta'(\kappa) < 0$ then (s_i^*, x_i^*) is asymptotically stable and if $f(s_i^*)F'_y(s_i^*) + \kappa\vartheta'(\kappa) > 0$ then (s_i^*, x_i^*) is unstable.

Proof. Calculation of the Jacobian matrix at (s_i^*, x_i^*) gives

$$J(s_i^*, x_i^*) = \begin{pmatrix} f(s_i^*)F'_y(s_i^*) - f(s_i^*) \\ -\kappa^2\vartheta'(\kappa) & \kappa\vartheta'(\kappa) \end{pmatrix} \tag{3.4}$$

and, consequently, the eigenvalues are

$$\begin{aligned} \lambda_{\pm} &= \frac{1}{2}[f(s_i^*)F'_y(s_i^*) + \kappa\vartheta'(\kappa) \\ &\pm \sqrt{(f(s_i^*)F'_y(s_i^*) + \kappa\vartheta'(\kappa))^2 - 4f(s_i^*)\vartheta'(\kappa)\kappa(F'_y(s_i^*) - \kappa)}]. \end{aligned} \tag{3.5}$$

□

From (3.2) and Theorem 3.3 we get the following corollaries:

Corollary 3.4 Assume (A-I)–(A-V) and (2.8). If $F'_y(s) < \kappa, s > 0$ then the system (2.4) has a unique equilibrium in \mathbf{R}_+^2 which cannot be a saddle point.

Corollary 3.5 Assume (A-I)–(A-V) and (2.8). If $F'_y(s) < -\kappa\vartheta'(\kappa)/f(s), s > 0$ then all unstable interior equilibria of the system (2.4) are saddle points.

4 Absence of limit cycles

In this section we investigate the global stability of equilibria. Similar problems have been considered in [16] and [21].

We shall derive functions and construct sets with respect to different vector fields later on. In order to indicate the underlying vector field the functions and sets are given subscripts referring to the formula in which the vector field is defined. We introduce the following notation.

Notation 4.1 Let (VF) be the vector field defined by

$$\begin{aligned} \dot{s} &= f(s, x) \\ \dot{x} &= g(s, x) \end{aligned} \tag{VF}$$

and let $H(s, x)$ be a C^1 -function. We denote the total time derivative of $H(s, x)$ with respect to the vector field (VF) by $\dot{H}_{(VF)}$.

Notation 4.2 Let (VF) be the vector field defined as above and let $\mathcal{A} \subset \mathbb{R}^2$. We use the notation $\mathcal{A}_{(VF)}$ to point out that the set \mathcal{A} is constructed with respect to the vector field (VF).

Theorem 4.3 Assume (A-I)–(A-V). Suppose that (2.4) has a unique interior equilibrium, (s^*, x^*) . If

$$(F_y(s) - F_y(s^*))(s - s^*) < 0, \quad s \neq s^*,$$

in some simply connected region, then the system (2.4) has no limit cycle lying completely in this region.

Proof. We introduce the Lyapunov-function

$$V(s, x) = \int_{s^*}^s \frac{\vartheta(x^*/s')}{f(s')} ds' + \int_{x^*}^x \frac{x' - F_y(s^*)}{x'} dx', \tag{4.1}$$

and get

$$\begin{aligned} \dot{V}_{(2.4)} &= \vartheta(x^*/s)(F_y(s) - x) - \vartheta(x/s)(F_y(s^*) - x) \\ &= \vartheta(x^*/s)(F_y(s) - x) - \vartheta(x^*/s)(F_y(s^*) - x) \\ &\quad + \vartheta(x^*/s)(F_y(s^*) - x) - \vartheta(x/s)(F_y(s^*) - x) \\ &= \vartheta(x^*/s)(F_y(s) - F_y(s^*)) + (\vartheta(x^*/s) - \vartheta(x/s))(x^* - x) \leq 0. \quad \square \end{aligned}$$

Example 4.4 We apply this result to the Eq. (1.2). The prey isocline is given by

$$F_y(s) = \frac{rs(1 - s/K) - ys^2}{cs} = \frac{1}{c} \left(rs + a_1r - \frac{r}{K}s^2 - \frac{ra_1}{K}s - ys^2 - a_1ys \right). \tag{4.2}$$

This is a parabola and hence the maximal derivative of $F_y(s)$ will be approached at the origin. We get

$$\sup_{s \geq 0} F'(s) = \frac{1}{c} \left(r - \frac{ra_1}{K} - a_1y \right), \tag{4.3}$$

and hence, if the number of generalist predators exceeds $r(1 - a_1/K)/a_1$ the system (1.2) cannot possess limit cycles and the unique interior fixed point is globally asymptotically stable.

5 Position of limit cycles

If the value of the Lyapunov function defined in (4.1) is large enough then all limit cycles due to dissipativity are contained in the region determined by the corresponding level curve of $V(s, x)$. In this section we shall consider systems of type (2.4) satisfying the following conditions.

$$\lim_{s \rightarrow 0} F_y(s) > x_i^* \tag{5.1}$$

$$\sup_{s \in [\min(s_i^*, K_m), K_1]} \vartheta \left(\frac{x_i^*}{s} \right) F_y(s) < \lim_{t \rightarrow 0} \vartheta(t) x_i^* \tag{5.2}$$

for some x_i^* . We give a numerical example below (Example 5.5) to show that the class of systems of type (2.4) which satisfies the conditions (A-I)–(A-V), (5.1)–(5.2) and possesses limit cycles is not empty.

Condition (5.1) guarantees that we can find an ϵ -region near the x -axis where $\dot{V}_{(2.4)} < 0$. Condition (5.2) is the analogous condition for the s -axis. The conditions (5.1)–(5.2) will then guarantee that the region defined below does not become infinite. Now define

$$\bar{V}_{(2.4)} = \inf\{m \geq 0 \mid V(s, x) > m \Rightarrow \dot{V}_{(2.4)} < 0\}. \tag{5.3}$$

From the definition of $\bar{V}_{(2.4)}$ we immediately get the following theorem.

Theorem 5.1 *Assume (A-I)–(A-V). Suppose the conditions (5.1) and (5.2) hold. Then the region*

$$\mathcal{V}_{(2.4)} = \{(s, x) \mid V(s, x) \leq \bar{V}_{(2.4)}\}$$

contains all limit cycles and interior equilibria of (2.4).

Proof. First note that the Lyapunov-function is positive definite, C^1 and satisfies $\lim_{s \rightarrow 0} V(s, x) = \infty$, and $\lim_{s \rightarrow \infty} V(s, x) = \infty$ by (A-I)–(A-V). The conditions $\lim_{x \rightarrow 0} V(s, x) = \infty$ and $\lim_{x \rightarrow \infty} V(s, x) = \infty$, are fulfilled by suitable behavior of the integrals of 1 and $1/x$. Conditions (5.1)–(5.2) and continuity of $\dot{V}_{(2.4)}$ implies that the region $\{(s, x) \in \mathbf{R}_+^2 \mid \dot{V}(s, x) \leq 0\}$ is a bounded region in the phase-plane, which does not intersect the boundary of \mathbf{R}_+^2 . This holds because conditions (A-II) and (A-IV) imply suitable behavior of $\dot{V}_{(2.4)}$ when $s \rightarrow \infty$ and $x \rightarrow \infty$. Now assume that a trajectory $(s(t), x(t))$ starts at $(s(0), x(0)) \in \mathbf{R}_+^2$ and that we have

$$V(s(t), x(t)) \geq \bar{V}_{(2.4)} + \epsilon, \epsilon > 0, \forall t \geq 0. \tag{5.4}$$

By definition (5.3) $\dot{V}_{(2.4)}$ is strictly negative in the region $\{(s, x) \mid V(s, x) \geq \bar{V}_{(2.4)} + \epsilon\}$. By continuity and suitable behavior near infinity we can find a value M , such that

$$\dot{V} \leq -M < 0 \tag{5.5}$$

whenever $(s, x) \in \{(s, x) \mid V(s, x) \geq \bar{V}_{(2.4)} + \epsilon\}$. Integration of (5.5) will contradict (5.4), and hence, no trajectories starting in \mathbf{R}_+^2 can have ω -limit sets outside $\mathcal{V}_{(2.4)}$. □

Lemma 5.2 *Assume (A-I)–(A-V) and (2.8). The rectangular region*

$$\mathcal{D}_{(2.4)} = \{(s, x) \mid 0 < s < K_1, 0 < x < K_1 \kappa\}$$

contains all limit cycles and interior equilibria of (2.4).

Remark 5.3 Observe that it is necessary to use Notation 4.2 in Lemma 5.2 because K_1 is dependent of the system (2.4).

Corollary 5.4 *Let the assumptions of theorem 5.1 hold. The intersection $\mathcal{V}_{(2.4)} \cap \mathcal{D}_{(2.4)}$ contains all limit cycles and interior equilibria of (2.4).*

In some cases of practical importance we may have some problems when we try to use Theorem 5.1. For example in the model (1.2) the condition (5.1) will not be satisfied, and hence, the region $\mathcal{V}_{(2.4)}$ will be infinite except for parameter values already guaranteeing absence of limit cycles. We remark that this difficulty can be eliminated by assuming that the functional response

$$f(s) = \frac{s}{s + a} \tag{5.6}$$

is an approximation of the more general functional response

$$f(s) = \frac{s^2}{s^2 + as + b} \tag{5.7}$$

for a small b .

Example 5.5 We show that there are systems possessing at least one limit cycle and satisfy (A-I)–(A-V), (5.1)–(5.2). This proves that the presented theorem and the analysis below are meaningful. We choose $h(s) = rs(1 - s/K)$, $y = 0$, $f(s) = s^2/(s^2 + a_1s + b_1)$ and $\vartheta(x/s) = q(1 - x/\gamma s)$. Conditions (A-I)–(A-IV) and (5.1) are clearly satisfied. A calculation corresponding to the calculation in Example 2.1 shows that condition (A-V) holds. Next we choose $r = 1$, $K = 1$, $c = 1$, $a_1 = 3/200$, $b_1 = 1/200$, $q = 1/5$, $\gamma = 1$. We solve the equation for the equilibria and get

$$F(s) = \frac{1}{s} (1 - s)(s^2 + a_1s + b_1) = s - s^3 - a_1s^2 + (a_1 - b_1)s + b_1 = 0.$$

This cubic equation may be solved, the only positive real solution of it is approximately $s^* \simeq 0.185051$. Further calculation shows that the equilibrium corresponding to this solution is unstable, and hence dissipativity gives that the system possesses at least one limit cycle. Now we have to verify the condition (5.2). We take the derivative of the function

$$\vartheta(x^*/s)F_y(s) - \lim_{t \rightarrow 0} \vartheta(t)x^*. \tag{5.8}$$

The zeros of the derivative of the function (5.8) correspond to the zeros of a certain fourth degree equation. By solving this equation we may show that it has exactly one positive zero ($s \simeq 0.585045$), and this zero corresponds to a maximum of the function (5.8). This maximum is approximately -0.00247826 , so condition (5.2) is satisfied. The regions $\mathcal{V}_{(2.4)}$ and $\mathcal{D}_{(2.4)}$ corresponding to this case are depicted in Fig. 1.

If we assume that the hunting efficiency of the generalist predators is low compared to the hunting efficiency of the specialist predators at low prey-densities we have that

$$\lim_{s \rightarrow 0} G(s) \simeq 0. \tag{5.9}$$

Under this condition the functional response (5.7) will give rise to a system of type (2.4) which satisfies the condition (5.1) for all y when $h(s) = s(1 - s/K)$ because then $\lim_{s \rightarrow 0} F_y(s) = \infty$ for all $y > 0$.

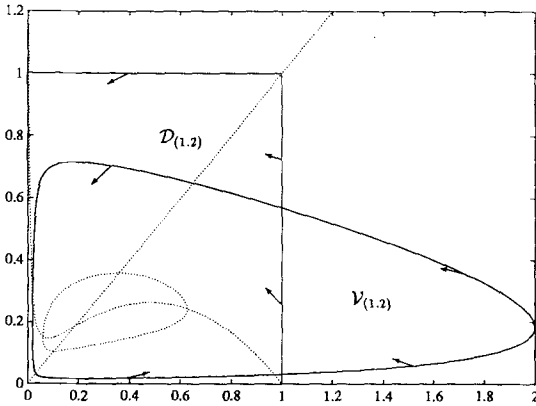


Fig. 1 The regions $\mathcal{V}_{(1,2)}$ and $\mathcal{D}_{(1,2)}$ for a system of type (1.2) with the more general functional response (5.7) $r = 1, K = 1, c = 1, \gamma = 1, y = 0, q = 1/5, a_1 = 0.015, b_1 = 0.005$

6 Qualitative behavior of limit cycles as the density of generalist predators varies

In this section we shall understand the qualitative behavior of the limit cycles as the density of the generalist predators is varied. The region $\mathcal{D}_{(2,4)}$ (Lemma 5.2) will in general shrink because $F_y(s) < F_{y_0}(s)$ when $y > y_0$. This does not, however, exclude more and more complicated behavior as shown by the following example.

Example 6.1 Consider the case when

$$G(s) = \frac{s^2 + a_1 s}{s^2 + b_2} \tag{6.1}$$

This corresponds to the situation in model (1.3). Suppose $nb_2 \ll a_1$. We have

$$\begin{aligned} \lim_{s \rightarrow 0} G(s) &= 0 \\ G(b_2/a_1) &\simeq 1 \\ &\vdots \\ G(nb_2/a_1) &\simeq n \\ G(a_1) &\simeq 2 \\ \lim_{s \rightarrow \infty} G(s) &= 1. \end{aligned}$$

This means that we may force the function $F_y(s)$ to change arbitrarily rapidly for small s as the generalist predator density increases.

Consider the model (1.3). We choose the parameter values $r = 1, K = 1, a = 1, c = 1, \gamma = 1$ and $b = 1/1000$. When $y = 0$ the system has a unique equilibrium which is globally asymptotically stable according to Theorem 4.3. If we choose $y = 2/30$ we have three interior equilibria and one of these is a saddle point. Note also that two equilibria along the s -axis has occurred. See Fig. 2 where we have sketched the isoclines for this set of parameter values in the cases $y = 0$ and $y = 2/30$. Note that the latter case does not possess limit cycles surrounding the equilibrium (s_3^*, x_3^*) (Notation 3.2). This can be shown with a region of type $\mathcal{D}_{(1,3)}$ determined by $0 < s < K_3, 0 < x < K_3 \kappa$ (recall Notation 3.1) and Theorem 4.3.

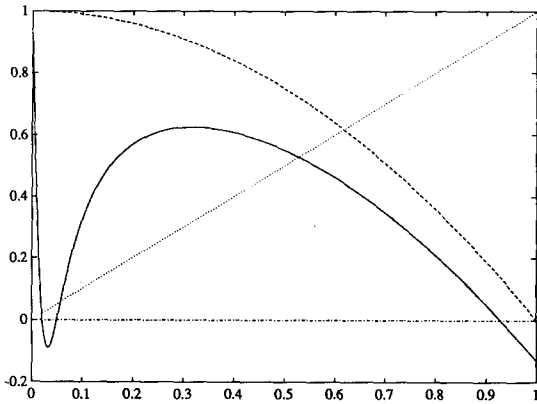


Fig. 2 Isoclines for the system (1.3) for the parameter values $r = 1$, $K = 1$, $a = 1$, $c = 1$, $\gamma = 1$ and $b = 1/1000$ for $y = 0$ and $y = 2/30$

For the rest of this section we restrict ourselves to the case when the half-saturation of the generalist predators is high compared to the number of small rodents, that is $G'(s) > 0$. We start with a quite general theorem.

Theorem 6.2 Define two systems according to

$$\begin{aligned} \dot{s} &= f(s)(F_1(s) - x) \\ \dot{x} &= x\vartheta(x/s) \end{aligned} \tag{6.2}$$

and

$$\begin{aligned} \dot{s} &= f(s)(F_2(s) - x) \\ \dot{x} &= x\vartheta(x/s). \end{aligned} \tag{6.3}$$

Assume (A-I)–(A-V) for (6.2)–(6.3). Suppose that, with respect to (s^*, x^*) ,

- (i) The conditions (5.1) and (5.2) are satisfied for (6.2).
- (ii) $(F_1(s) - F_2(s))(s - s^*) < 0$, $s \neq s^*$,

then, with respect to (s^*, x^*) ,

- (i) The conditions (5.1) and (5.2) are satisfied for (6.3).
- (ii) The region $\mathcal{V}_{(6.2)}$ covers completely $\mathcal{V}_{(6.3)}$.

Proof. (i) We have

$$\begin{aligned} \dot{V}_{(6.3)} - \dot{V}_{(6.2)} &= \vartheta(x^*/s)(F_2(s) - F_2(s^*)) + (\vartheta(x^*/s) - \vartheta(x/s))(x^* - x) \\ &\quad - \vartheta(x^*/s)(F_1(s) - F_1(s^*)) - (\vartheta(x^*/s) - \vartheta(x/s))(x^* - x) \\ &= \vartheta(x^*/s)(F_2(s) - F_1(s)) \leq 0, \end{aligned}$$

so

$$\dot{V}_{(6.3)} \leq \dot{V}_{(6.2)}$$

and hence

$$\begin{aligned} \{(s, x) \mid \dot{V}_{(6.2)}(s, x) \leq 0\} &\supseteq \{(s, x) \mid \dot{V}_{(6.3)}(s, x) \leq 0\} \\ \mathcal{V}_{(6.2)} &\supseteq \mathcal{V}_{(6.3)}. \end{aligned}$$

□

We shall need the next definition for the formulation of the next theorem.

Definition 6.3 Let $M \subset \mathbb{R}^2_+$. The set $\{M\}_k$ is defined by the relation

$$(s, x) \in M \Leftrightarrow (ks, kx) \in \{M\}_k. \tag{6.4}$$

Theorem 6.4 Assume (A-I)–(A-V). Suppose that $G'(s) \geq 0, y \geq y_0$. Let $(s_y^*, x_y^*), (s_{y_0}^*, x_{y_0}^*)$ be interior equilibria of the two systems

$$\begin{aligned} \dot{s} &= f(s)(F_{y_0}(s) - x) \\ \dot{x} &= xg(x/s), \end{aligned} \tag{6.5}$$

and

$$\begin{aligned} \dot{s} &= f^*(s)(F_y(s) - x) \\ \dot{x} &= xg(x/s), \end{aligned} \tag{6.6}$$

respectively, satisfying $s_y^* \leq s_{y_0}^*$. If (5.1) and (5.2) are satisfied for (6.5) and $f^*((s_y^*/s_{y_0}^*)s) = f(s)$ then

- (i) The conditions (5.1) and (5.2) are satisfied for (6.6).
- (ii) The region $\{\mathcal{V}_{(6.6)} \cap \mathcal{D}_{(6.6)}\}_{s_{y_0}^*/s_y^*}$ will be completely contained in the region $\mathcal{V}_{(6.5)} \cap \mathcal{D}_{(6.5)}$.
- (iii) Put $\mathcal{A} = \{s > 0 \mid F'_{y_0}(s) \geq 0\}$. If $\inf_{s \in \mathcal{A}} G'(s) > 0$ then there exists a \bar{y} such that if $y > \bar{y}$ then the system (6.6) has an equilibrium which is globally asymptotically stable.

Proof. We transform the system

$$\begin{aligned} \dot{\hat{s}} &= f^*(\hat{s})(F_y(\hat{s}) - \hat{x}) \\ \dot{\hat{x}} &= \hat{x}g(\hat{x}/\hat{s}), \end{aligned} \tag{6.7}$$

by the linear transform

$$s = \frac{s_{y_0}^*}{s_y^*} \hat{s}, \quad x = \frac{x_{y_0}^*}{x_y^*} \hat{x} \tag{6.8}$$

and arrive at

$$\begin{aligned} \dot{s} &= f(s)(\tilde{F}(s) - x) \\ \dot{x} &= xg(x/s), \end{aligned} \tag{6.9}$$

where we have used the fact that

$$f^*\left(\frac{s_y^*}{s_{y_0}^*} s\right) = f(s) \tag{6.10}$$

and defined $\tilde{F}(s)$ as

$$\tilde{F}(s) = \frac{s_{y_0}^*}{s_y^*} F_y\left(\frac{s_y^*}{s_{y_0}^*} s\right). \tag{6.11}$$

Now replace the system (6.2) and (6.3) in Theorem 6.2 by the systems (6.5) and (6.9), respectively. We have to verify the conditions (i)–(ii) of Theorem 6.2. The condition (i) follows because of our assumptions.

To verify condition (ii) observe that

$$\tilde{F}(s_{y_0}^*) = \frac{s_{y_0}^*}{s_y^*} F_y(s_y^*) = \frac{s_{y_0}^*}{s_y^*} x_y^* = s_{y_0}^* \kappa = x_{y_0}^* = F_{y_0}(s_{y_0}^*)$$

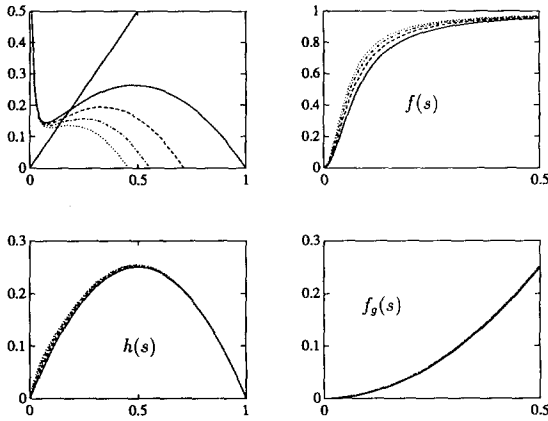


Fig. 3 Simultaneous changes of the functions $f(s)$, $h(s)$, $f_g(s)$ in the model (2.1) for the ideal case described by Theorem 6.4 together with the changes in the isoclines for $y = 0$ (solid), $y = 0.4$ (dashed), 0.8 (dashdotted), 1.2 (dotted). The system corresponding to $y = 0$ is (1.2) with the more general functional response (5.7) and $r = 1$, $K = 1$, $c = 1$, $\gamma = 1$, $a_1 = 0.015$, $b_1 = 0.005$

and

$$0 < G'(s) = F'_{y_0}(s) - F'_y(s) = \frac{d}{ds} \left(F_{y_0}(s) - \frac{s^*_{y_0}}{s^*_y} F_y \left(\frac{s^*_y}{s^*_{y_0}} s \right) \right) = \frac{d}{ds} (F_{y_0}(s) - \tilde{F}(s)).$$

To prove assertion (iii) we may note that as the density of generalist predators increases we shall sooner or later have $F'_y(s) < 0$. \square

Example 6.5 If we use the model (1.2) the condition $G'(s) > 0$ of Theorem 6.4 is satisfied. However, the condition (5.1) is not generally satisfied, but we have already noted that this difficulty can be removed using the more general specialist predator functional response (5.7) (Sect. 5).

Remark 6.6 Theorem 6.4 describes an ideal case when the motion of the limit cycles is expected to be most regular. It states that the functions $h(s)$, $f(s)$ and $f_g(s)$ in the system (2.1) have to follow the variation in the generalist predator density in a suitable sense. These variations are depicted in Fig. 3 for the system (1.2) with the more general functional response (5.7).

7 Construction of multiple limit cycles

The Hopf-bifurcation stability formula see e.g. [3] enables us to construct multiple limit cycles in the model (1.3). Similar ideas have been used to construct multiple limit cycles in other systems cf. [6, 26, 27]. Our example will show that this is possible without assuming that the system (1.3) has several interior equilibria.

We choose the parameters involved in the model (1.3) so that the system undergoes a Hopf-bifurcation at the equilibrium (s_i^*, x_i^*) . The choice

$$f(s_i^*) = 1 \tag{7.1}$$

$$\kappa = 1 \tag{7.2}$$

$$\mathfrak{J}'(\kappa) = -1/2 \tag{7.3}$$

$$F'_y(s_i^*) = 1/2 \tag{7.4}$$

$$\mathfrak{J}^{(n)}(\kappa) = 0, \quad n > 1 \tag{7.5}$$

$$\gamma = 1 \tag{7.6}$$

will simplify our work with the coordinate transforms required for using the Hopf-bifurcation stability formula.

By (7.2) we have $x_i^* = s_i^*$. We move the equilibrium (s_i^*, s_i^*) to the origin by the affine transform

$$\begin{aligned} \xi &= s = s_i^* \\ \eta &= x - s_i^* \end{aligned} \tag{7.7}$$

and the system (2.4) transforms into

$$\begin{aligned} \dot{\xi} &= f(\xi + s_i^*)[F_y(\xi + s_i^*) - \eta - s_i^*] \\ \dot{\eta} &= (\eta + s_i^*)\vartheta\left(\frac{\eta + s_i^*}{\xi + s_i^*}\right). \end{aligned} \tag{7.8}$$

In order to get the standard form of (2.4) we choose the further transform

$$\begin{aligned} u &= \xi - \eta \\ v &= \eta \end{aligned} \tag{7.9}$$

and obtain

$$\begin{aligned} \dot{u} &= f(u + v + s_i^*)[F_y(u + v + s_i^*) - v - s_i^*] - (\eta + s_i^*)\vartheta\left(\frac{v + s_i^*}{u + v + s_i^*}\right) \\ \dot{v} &= (\eta + s_i^*)\vartheta\left(\frac{v + s_i^*}{u + v + s_i^*}\right). \end{aligned} \tag{7.10}$$

We expand all functions in Taylor series, making especially use of assumption (7.5) and get as a third order approximation of the system near (s_i^*, s_i^*)

$$\begin{aligned} \dot{u} &= -\frac{1}{2}\left(v - \frac{u^2}{s_i^*} + \frac{u^3}{(s_i^*)^2} + \frac{u^2v}{(s_i^*)^2}\right) + \frac{F_y''(s_i^*)}{2}(u + v)^2 \\ &\quad + \frac{f''(s_i^*)}{4}(u^3 + u^2v - uv^2 - v^3) + \frac{F_y'''(s_i^*)}{6}(u + v)^3 \\ &\quad + \frac{f'(s_i^*)}{2}(u^2 - v^2) + \frac{F_y''(s_i^*)f'(s_i^*)}{2}(u + v)^3 \\ \dot{v} &= \frac{1}{2}\left(u - \frac{u^2}{s_i^*} + \frac{u^3}{(s_i^*)^2} + \frac{u^2v}{(s_i^*)^2}\right). \end{aligned}$$

This expression is now in standard form. This means that we can apply the Hopf bifurcation stability formula to this expression. We get

$$\begin{aligned} \alpha &= \frac{1}{16s_i^*} [4F_y''(s_i^*) + 4s_i^*(F_y''(s_i^*))^2 + s_i^*f''(s_i^*) \\ &\quad + 2s_i^*F_y'''(s_i^*) + 2f'(s_i^*) + 6s_i^*F_y''(s_i^*)f'(s_i^*)]. \end{aligned} \tag{7.11}$$

The sign of α determines the stability of (s_i^*, s_i^*) .

The formula (7.11) is quite complicated and we start by choosing $s^* = 1$, $r = K$ and $a_1 \simeq 0$. When $a_1 \simeq 0$ both derivatives of $f(s)$ in the expression vanish and we have

$$\alpha \simeq \frac{1}{8}[2F_y''(1) + 2(F_y''(1))^2 + F_y'''(1)] \tag{7.12}$$

$$F_y(s) \simeq s(K - s) - y \frac{s^2}{s^2 + b_2}. \tag{7.13}$$

The first term of the Taylor expansion of $F_y(s)$ must equal one and according to the assumptions $\kappa = 1$ and $s^* = 1$ and we have

$$-1 + K - \frac{y}{1 + b_2} = 1. \tag{7.14}$$

We may solve K from this equation. According to the assumption (7.4) we also know the coefficient of the second term in the Taylor expansion of F_y . We solve y from the obtained equation and get

$$y = \frac{1}{2} \frac{(1 + b_2)^2}{1 - b_2}. \tag{7.15}$$

Now the Taylor expansion of F_y looks like

$$F_y(s) = 1 + \frac{1}{2}(s - 1) + \frac{-2 + 3b_2 + b_2^2}{2 - 2b_2^2}(s - 1)^2 - \frac{2b_2}{(1 + b_2)^2}(s - 1)^3 + O((s - 1)^4). \tag{7.16}$$

In order to make α positive, choose $b_2 = 3/4$ and we have $\alpha \simeq 47/49 > 0$. This choice will not lead to several interior equilibria because $F_y(s) - s = 0$ iff

$$(1 - s)s(27 - 28s + 8s^2) = 0. \tag{7.17}$$

Now if a_1 is slightly greater than zero the corresponding system will undergo a Hopf bifurcation so that all equilibria are unstable for this choice of parameters. Because the system was dissipative the system has at least one externally stable (from the outside stable cf. [28]) limit cycle. If we perturb the system so that the stability of the equilibrium changes one unstable limit cycle appears due to the Hopf bifurcation theorem. This perturbed system possesses at least two limit cycles. The situation is depicted in Fig. 4 for the system (1.3) in the case

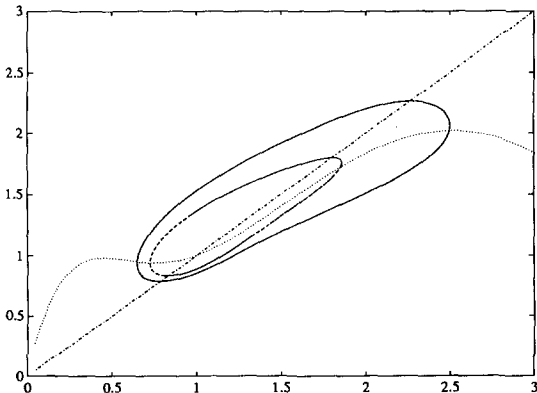


Fig. 4 Multiple limit cycles for the system (1.3) in the case $r = 5\frac{1}{2}$, $K = 5\frac{1}{2}$, $c = 1$, $\gamma = 1$, $y = 49/8$, $a_1 = 1/100$, $b_2 = 3/4$, $q = 5/8$

$r = 5\frac{1}{2}, K = 5\frac{1}{2}, c = 1, \gamma = 1, y = 49/8, a_1 = 1/100, b_2 = 3/4, q = 5/8$. The interior limit cycle is unstable and calculated by integrating the system backwards.

8 Construction of complicated global bifurcations

The construction in Sect. 7 enables us to construct a complicated global bifurcation in a related system. Consider the system

$$\begin{aligned} \dot{s} &= rs(1 - s/K) - cx \frac{s}{s + a_1} - y \frac{s^2}{s^2 + b_2} - \frac{z}{\pi} \left(\arctan(-w(s - s_0)) + \frac{\pi}{2} \right) \\ \dot{x} &= qx(1 - x/\gamma s). \end{aligned} \tag{8.1}$$

This system may be written in the usual form (2.4). We shall choose the parameters $r = 5\frac{1}{2}, K = 5\frac{1}{2}, \gamma = 1, c = 1, y = 49/8, a_1 = 1/100, b_2 = 3/4, w = 1500, s_0 = 0.99, z = 0.01$ to construct complicated bifurcations with respect to the parameter $q \approx 0.682$. First consider the rough view of the system (Fig. 5) where we have sketched the isoclines and the unstable manifold of the saddle point $(K_1, 0)$.

If we magnify the small rectangle in Fig. 5 we note that the system (8.1) has a saddle point and a couple of limit cycles surrounding it (Fig. 6). If we increase the value of q the limit cycles will coalesce into each other at some value q^* .

However, the bifurcation which appears as the limit cycles coalesce is not only a limit cycle bifurcation, because the stable manifolds of (s_2^*, x_2^*) (Notation 3.2) and the unstable manifold of $(K_1, 0)$ (Notation 3.1) are involved in the bifurcation. This is illustrated in Fig. 7 where we have plotted successive Poincaré plots of the stable and unstable manifolds in the cross-section $s = 0.998$ for four different values of q (horizontal axis). The x -values are plotted against the vertical axis.

When the limit cycles coalesce infinitely many saddle connection bifurcations will occur in some interval $[q^*, q^* + \epsilon]$. That is, the limit cycle bifurcation-value q^* is, in fact, an accumulation point of other bifurcations. The phenomenon is described in more detail in [3]. Hence the related system (8.1) undergoes a complicated global bifurcation scheme in the interval $[q^*, q^* + \epsilon]$. We note that nothing excludes this phenomenon in the predator-prey model (1.3), and that the numerical evidence presented here does not establish the phenomenon for the used parameter values.

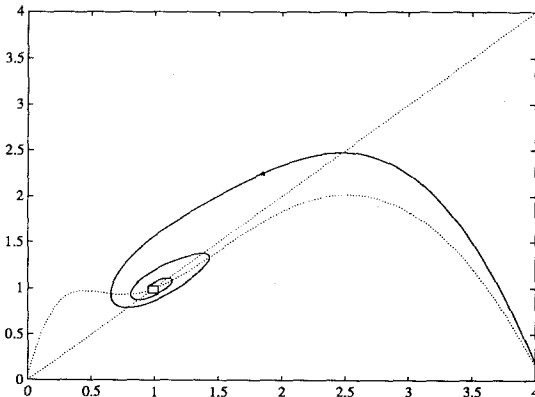


Fig. 5 Rough view of the system (8.29) in the case $r = 5\frac{1}{2}, K = 5\frac{1}{2}, c = 1, \gamma = 1, y = 49/8, a_1 = 1/100, b_2 = 3/4, q = 1/1.465, s_0 = 0.99, w = 1500, z = 0.01$

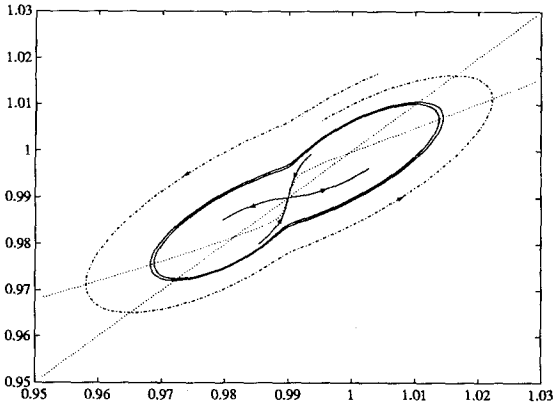


Fig. 6 Multiple limit cycles outside a saddle point in the system (8.29) in the case $r = 5\frac{1}{2}$, $K = 5\frac{1}{2}$, $c = 1$, $\gamma = 1$, $y = 49/8$, $a_1 = 1/100$, $b_2 = 3/4$, $q = 1/1.465$, $s_0 = 0.99$, $w = 1500$, $z = 0.01$

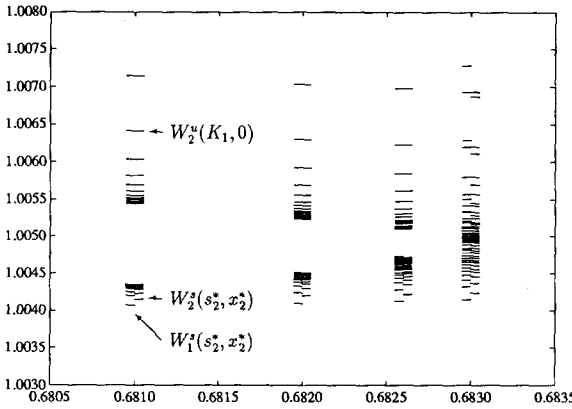


Fig. 7 Successive Poincaré-plots of the stable manifolds of (s_2^*, x_2^*) and the unstable manifold of $(K_1, 0)$ in the cross-section $s = 0.998$ against the parameter value of q (horizontal axis) and the value of x (vertical axis) for the system (8.29) in the case $r = 5\frac{1}{2}$, $K = 5\frac{1}{2}$, $c = 1$, $\gamma = 1$, $y = 49/8$, $a_1 = 1/100$, $b_2 = 3/4$, $s_0 = 0.99$, $w = 1500$, $z = 0.01$

9 Remarks about a related predator-prey model

Huang [10, 11, 12], Huang and Merrill [13], Kuang [18, 20], Kuang and Freedman [19] have investigated a system which is quite similar to ours. We review some results concerning these systems and present some comparison results.

9.1 Definition and fundamental properties

Gause-type predator-prey models of type

$$\begin{aligned} \dot{s} &= f(s)(F_y(s) - \pi(x)) \\ \dot{x} &= \varrho(x)\psi(s). \end{aligned} \tag{9.1}$$

are (especially when $\psi'(s) > 0$) more well-known than our system (2.7). They are more close to our system than the separable system

$$\begin{aligned} \dot{s} &= f(s)(F_y(s_1^*) - x) \\ \dot{x} &= x\vartheta(x_1^*/s) \end{aligned} \tag{9.2}$$

corresponding to the Lyapunov-function defined in (4.1) and hence it may be possible to get some results about (4.2) comparing it to the system (9.1). We shall assume that the Gause-type predator-prey model satisfies the following general conditions:

(G-I) All the functions f, π, ϱ and ψ are continuously differentiable of any required order (At least C^1). The function F_y is continuously differentiable of any required order at all other points except possibly at the origin, but $\lim_{s \rightarrow 0} f(s)F_y(s) = 0$ and $\lim_{s \rightarrow 0} F_y(s) > 0$.

(G-II) There exists a point K such that $F_y(s) < 0$ if $s > K$.

(G-III) The functions f, π, ϱ are increasing and have unique zeros at zero.

Theorem 9.1 *Assume (G-I)–(G-III). If $s(0) > 0$ and $x(0) > 0$ the solutions $s(t)$ and $x(t)$ of (9.1) remain positive, if moreover $\psi(s) < 0$ for $s < s$, $F_y(s) > 0$ and*

$$\int_{\pi^{-1}(F_y(s))}^{\infty} \frac{dx}{\varrho(x)} = \infty. \tag{9.3}$$

then the system (9.1) is dissipative.

Remark 9.2 The condition (9.3) seems to be important only for the proof presented here, so there may be some possibilities to improve the theorem. However, we shall mainly work with $\varrho(x) = x$, and hence the theorem is enough for our purposes. We also remark that the condition $\psi(s) < 0$ for small s is essential for dissipativity and cannot be removed.

Proof. The axes consist of different trajectories of the system, and hence, the solutions remain positive by uniqueness of solutions. To prove dissipativity, first note that all solutions will enter the infinite rectangular region $0 < s < s_{\max}, s_{\max} > K$. Now introduce the Lyapunov level curves

$$V(s, x) = \int_s^s \frac{ds}{f(s)} + \int_{\pi^{-1}(F_y(s))}^x \frac{dx}{\varrho(x)} \tag{9.4}$$

in the infinite quadratic region $s > s, x > \pi^{-1}(F_y(s))$. Now choose

$$\hat{x} = \max \left(\sup_{s < s < s_{\max}} \pi^{-1}(F_y(s) + \psi(s)), \pi^{-1}(F_y(s)) \right) \tag{9.5}$$

and we have that $\dot{V} < 0$ for $x > \hat{x}$. Put

$$V_0 = \int_s^{s_{\max}} \frac{ds}{f(s)} + \int_{\pi^{-1}(F_y(s))}^{\hat{x}} \frac{dx}{\varrho(x)}, \tag{9.6}$$

and by (9.3) we may choose

$$x_{\max} = \left\{ x \mid \int_{\pi^{-1}(F_y(s))}^x \frac{dx}{\varrho(x)} = V_0 \right\}. \tag{9.7}$$

By the implicit function theorem the level curve $V(s, x) = V_0$ defines a function $x = v(s)$, which by positivity of $\varrho(x)$ and $f(s)$, is unique and strictly decreasing, for $s < s < s_{\max}$. Now all trajectories will enter the region

$$\mathcal{R} = \{(s, x) \mid 0 < s < s, 0 < x < x_{\max}\} \cup \{(s, x) \mid s < s < s_{\max}, 0 < x < v(s)\}. \quad \square$$

The similarities between the system (9.1) and generalized Liénard equations:

$$\begin{aligned} \dot{x} &= \varphi(y) - F(x) \\ \dot{y} &= -g(x) \end{aligned} \tag{9.8}$$

have been used to apply a theorem by Zhang [29] in order to prove a uniqueness of limit cycles result for the Gause-type predator-prey model (9.1).

Theorem 9.3 (Huang [10], Kuang and Freedman [19]) *Assume (G-I)–(G-III). Suppose that*

(i) *The function ψ is strictly increasing and has a unique zero at s ; $\lim_{x \rightarrow \infty} \pi(x) = \infty$; the function $F_y(s)$ has a unique zero at $K_1 > s$ such that*

$$(s - K_1)F_y(s) < 0, \quad s \neq K_1.$$

(ii) *The function*

$$\frac{-F'_y(s)f(s)}{\psi(s)}$$

is non-decreasing for $s \neq s$.

Then the system (9.1) has at most one limit cycle, and if it exists it is stable.

The fact that the system (9.1) has so well-known dynamics under the above conditions will be used in Sect. 9.2. Note that the first condition is a condition which is expected to be valid for usual predator-prey systems of type (9.1), the last one is needed for the proof of the uniqueness of the limit cycle.

9.2 Comparison of our predator-prey system with a system of Gause-type

Suppose that $\vartheta(t)$ is a decreasing function defined on the entire real line. The system

$$\begin{aligned} \dot{s} &= f(s)(F_y(s) - x) \\ \dot{x} &= x\vartheta(F_y(s)/s) \end{aligned} \tag{9.9}$$

is a rotation of the vector field (2.4) because

$$\begin{vmatrix} \dot{s}_{(2.4)} & \dot{x}_{(2.4)} \\ \dot{s}_{(9.9)} & \dot{x}_{(9.9)} \end{vmatrix} = x f(s)(F_y(s) - x) \left(\vartheta \left(\frac{F_y(s)}{s} \right) - \vartheta \left(\frac{x}{s} \right) \right) \leq 0, \tag{9.10}$$

where $\dot{s}_{(2.4)}$, $\dot{x}_{(2.4)}$, $\dot{s}_{(9.9)}$ and $\dot{x}_{(9.9)}$ are defined by (2.4) and (9.9), respectively. The theory of general rotated vector fields (cf. [28]) gives:

Lemma 9.4 *Assume (A-I)–(A-V) for (2.4), (G-I)–(G-III) for (9.9) and that $\vartheta(t)$ is a decreasing function defined on the entire real line. Closed trajectories of the system (2.4) and the system (9.9) do not intersect. Moreover, equilibria of (2.4) and (9.9) have the same indexes.*

The systems (2.4) and (9.9) are dissipative according to Theorem 2.3 and Theorem 9.1, respectively. When we combine dissipativity of the systems (2.4) and (9.9) with the theory of general rotated vector fields we get:

Theorem 9.5 *Assume (A-I)–(A-V) for (2.4), (G-I)–(G-III), (9.3) for (9.9) and that $\mathfrak{g}(t)$ is a decreasing function defined on the entire real line. If $\lim_{s \rightarrow 0} F_y(s) > 0$, the vector field (2.4) has no limit cycles surrounding all limit cycles and interior equilibria of (9.9).*

Proof. First note that none of the equilibria along the s -axis of the system (9.9) are stable. If the system (2.4) does not have a limit cycle the theorem holds, i.e. assume the existence of at least one limit cycle in the system (2.4). The region between the boundary of \mathcal{R} (definition in the proof of Theorem 9.1) and the outermost limit cycle of (2.4) forms a trapping region for the system (9.9), and hence the existence of a limit cycle or an interior equilibrium outside the outermost limit cycle of (2.4) is established by the Poincaré–Bendixson theorem. \square

We can also apply Theorem 9.3 to show uniqueness of limit cycles of (9.9) if the following conditions hold ($s > 0$):

$$F'_y(s) < F_y(s)/s \tag{9.11}$$

$$F_y(s)(s - K_1) < 0, \quad s \neq K_1, \tag{9.12}$$

$$\frac{d}{ds} \frac{F'_y(s)f(s)}{\mathfrak{g}\left(\frac{F_y(s)}{s}\right)} \leq 0, \quad s \neq s. \tag{9.13}$$

The condition (9.11) implies that the function $\psi(s) = \mathfrak{g}(F_y(s)/s)$ is strictly increasing. This case is the most investigated case, because this is ecologically the most interesting. There are, however, some works about other cases (cf. [26]). If the system satisfies the condition (9.11) we also have by Corollary 3.4 and Lemma 9.4 that the systems (2.4) and (9.9) have a unique equilibrium which cannot be a saddle point. From the above uniqueness assumptions we get the following corollary.

Corollary 9.6 *Assume (A-I)–(A-V) for (2.4), (G-I)–(G-III) and (9.3) for (9.9) and that $\mathfrak{g}(t)$ is a decreasing function defined on the entire real line. If the conditions of theorem 9.3 hold for the system (9.9), then all limit cycles of (2.4) are contained in the unique limit cycle of (9.9).*

As a final remark we also note that the motion of the limit cycles in the model (9.1) can be followed quite easily in certain situations.

Two systems of type (9.1) with different $F : s$ are rotated with respect to each other if $\psi(s)$ is a strictly increasing function with a unique zero at $s = s^*$ and $(F_1(s) - F_2(s))(s - s^*) \geq 0$ because

$$\left| \frac{f(s)(F_1(s) - \pi(x)) \varrho(x)\psi(s)}{f(s)(F_2(s) - \pi(x)) \varrho(x)\psi(s)} \right| = \varrho(x)f(s)\psi(s)(F_1(s) - F_2(s)) \geq 0. \tag{9.14}$$

Moreover, if these functions satisfy the uniqueness conditions in Theorem 9.3 for both systems, then we know by the theory of general rotated vector fields (cf. [28]), that the unique limit cycle of system corresponding to F_2 will be contained in the unique limit cycle in the system corresponding to F_1 .

10 Summary

We have analyzed the predator-prey model

$$\begin{aligned}\dot{s} &= h(s) - xf(s) - yf_g(s) \\ \dot{x} &= xg(x/s).\end{aligned}\tag{10.1}$$

We have shown that predator-prey cycles described by this model are likely to be stabilized by generalist predation as observed in Fennoscandia (Sect. 1) if the half-saturation of the generalist predators is high compared to the number of small rodents. This result includes the following partial results:

(i) We put up conditions guaranteeing that all the limit cycles of the system are inside a level curve of a Lyapunov function.

(ii) We showed that if these conditions are fulfilled for some generalist predator density, then they are also satisfied for a higher generalist predator density.

(iii) We prove that there exists an ideal case so that if suitable simultaneous changes do occur in the functions $h(s)$, $f(s)$, and $f_g(s)$ as the density of the generalist predator increases then the level curve containing the limit cycles at a higher generalist predator density can be moved so that it lies completely inside the corresponding level curve at lower generalist predator density.

(iv) We show that if the generalist predator density is sufficiently high, then the system (10.1) has an equilibrium which is globally asymptotically stable.

We give examples showing that if the half-saturation of the generalist predators is not high compared to the number of small rodents, then multiple equilibria and multiple limit cycles may occur as the density of generalist predators increases. Complicated global bifurcations may also be constructed in related systems.

We compare our system to a more well-known class of predator-prey systems, the Gause-type predator-prey models (Sect. 9). The most important result of this comparison is that the outermost limit cycle of a special Gause-type predator-prey model will contain all the limit cycles of our model.

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